Themes and Concepts of Biology

By the end of this section, you will be able to do the following:

- Identify and describe the properties of life
- Describe the levels of organization among living things
- Recognize and interpret a phylogenetic tree
- List examples of different subdisciplines in biology

Biology is the science that studies life, but what exactly is life? This may sound like a silly question with an obvious response, but it is not always easy to define life. For example, a branch of biology called virology studies viruses, which exhibit some of the characteristics of living entities but lack others. Although viruses can attack living organisms, cause diseases, and even reproduce, they do not meet the criteria that biologists use to define life. Consequently, virologists are not biologists, strictly speaking. Similarly, some biologists study the early molecular evolution that gave rise to life. Since the events that preceded life are not biological events, these scientists are also excluded from biology in the strict sense of the term.

From its earliest beginnings, biology has wrestled with three questions: What are the shared properties that make something “alive”? Once we know something is alive, how do we find meaningful

levels of organization in its structure? Finally, when faced with the remarkable diversity of life, how do we organize the different kinds of organisms so that we can better understand them? As scientists discover new organisms every day, biologists continue to seek answers to these and other questions.

A toad represents a highly organized structure consisting of cells, tissues, organs, and organ systems. (credit: “Ivengo”/Wikimedia Commons) The leaves of this sensitive plant (*Mimosa pudica*) will instantly droop and fold when touched. After a few minutes, the plant returns to normal. (credit: Alex Lomas) Although no two look alike, these kittens have inherited genes from both parents and share many of the same characteristics. (credit: Rocky Mountain Feline Rescue) Polar bears (*Ursus maritimus*) and other mammals living in ice-covered regions maintain their body temperature by generating heat and reducing heat loss through thick fur and a dense layer of fat under their skin. (credit: “longhorndave”/Flickr) The California condor (*Gymnogyps californianus*) uses chemical energy derived from food to power flight. California condors are an endangered species. This bird has a wing tag that helps biologists identify the individual. (credit: Pacific Southwest Region U.S. Fish and Wildlife Service)

Properties of Life

All living organisms share several key characteristics or functions: order, sensitivity or response to the environment, reproduction, adaptation, growth and development, regulation, homeostasis, energy processing, and evolution. When viewed together, these nine characteristics serve to define life.

Order

Organisms are highly organized, coordinated structures that consist of one or more cells. Even very simple, single-celled organisms are remarkably complex: inside each cell, atoms comprise molecules. These in turn comprise cell organelles and other cellular inclusions. In multicellular organisms ([link]), similar cells form tissues. Tissues, in turn, collaborate to create organs (body structures with a distinct function). Organs work

together to form organ systems.

Sensitivity or Response to Stimuli

Organisms respond to diverse stimuli. For example, plants can bend toward a source of light, climb on fences and walls, or respond to touch ([link]). Even tiny bacteria can move toward or away from chemicals (a process called *chemotaxis*) or light (*phototaxis*). Movement toward a stimulus is a positive response, while movement away from a stimulus is a negative response.

Link to Learning

Watch this video to see how plants respond to a

stimulus—from opening to light, to wrapping a tendril around a branch, to capturing prey.

Reproduction

Single-celled organisms reproduce by first duplicating their DNA, and then dividing it equally as the cell prepares to divide to form two new cells. Multicellular organisms often produce specialized reproductive germline, gamete, oocyte, and sperm cells. After fertilization (the fusion of an oocyte and a sperm cell), a new individual develops. When reproduction occurs, DNA containing genes are passed along to an organism's offspring. These genes ensure that the offspring will belong to the same species and will have similar characteristics, such as size and shape.

Growth and Development

Organisms grow and develop as a result of genes providing specific instructions that will direct cellular growth and development. This ensures that a species' young ([link]) will grow up to exhibit many of the same characteristics as its parents.

Regulation

Even the smallest organisms are complex and require multiple regulatory mechanisms to coordinate internal functions, respond to stimuli, and cope with environmental stresses. Two examples of internal functions regulated in an organism are nutrient transport and blood flow. Organs (groups of tissues working together) perform specific functions, such as carrying oxygen throughout the body, removing wastes, delivering nutrients to every cell, and cooling the body.

Homeostasis

In order to function properly, cells require appropriate conditions such as proper temperature, pH, and appropriate concentration of diverse chemicals. These conditions may, however, change from one moment to the next. Organisms are able to maintain internal conditions within a narrow range almost constantly, despite environmental changes, through **homeostasis** (literally, “steady state”). For example, an organism needs to regulate body temperature through the thermoregulation process. Organisms that live in cold climates, such as the polar bear ([link]), have body structures that help them withstand low temperatures and conserve body heat. Structures that aid in this type of insulation include fur, feathers, blubber, and fat. In hot climates, organisms have methods (such as perspiration in humans or panting in dogs) that help them to shed excess body heat.

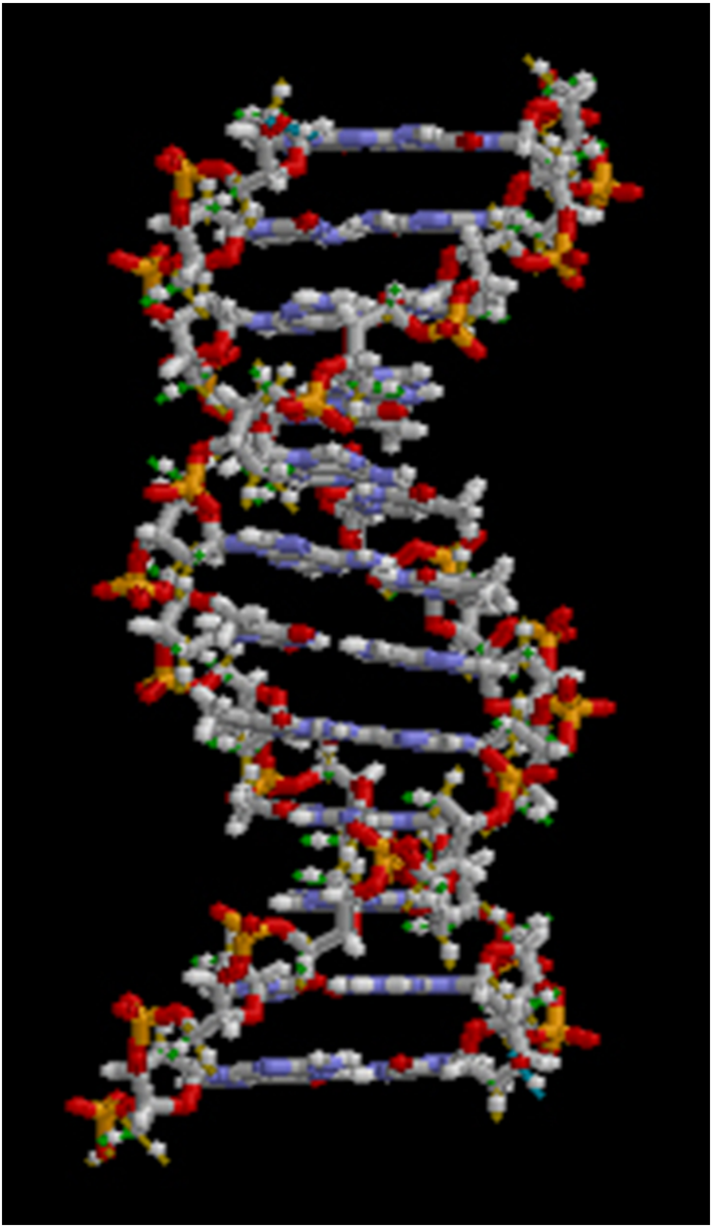
Energy Processing

All organisms use a source of energy for their metabolic activities. Some organisms capture energy from the sun and convert it into chemical energy in food. Others use chemical energy in molecules they take in as food ([link]).

All molecules, including this DNA molecule, are comprised of atoms. (credit: “brian0918”/ Wikimedia Commons)

Levels of Organization of Living Things

Living things are highly organized and structured, following a hierarchy that we can examine on a scale from small to large. The **atom** is the smallest and most fundamental unit of matter. It consists of a nucleus surrounded by electrons. Atoms form molecules. A **molecule** is a chemical structure consisting of at least two atoms held together by one or more chemical bonds. Many molecules that are biologically important are **macromolecules**, large molecules that are typically formed by polymerization (a polymer is a large molecule that is made by combining smaller units called monomers, which are simpler than macromolecules). An example of a macromolecule is deoxyribonucleic acid (DNA) ([link]), which contains the instructions for the structure and functioning of all living organisms.



Link to Learning

Watch this video that animates the three-dimensional structure of the DNA molecule in [link].

Some cells contain aggregates of macromolecules surrounded by membranes. We call these **organelles**. Organelles are small structures that exist within cells. Examples of organelles include mitochondria and chloroplasts, which carry out indispensable functions: mitochondria produce energy to power the cell, while chloroplasts enable green plants to utilize the energy in sunlight to make sugars. All living things are made of cells. The **cell** itself is the smallest fundamental unit of structure and function in living organisms. (This requirement is why scientists do not consider viruses living: they are not made of cells. To make new viruses, they have to invade and hijack the reproductive mechanism of a living cell. Only then can they obtain the materials they need to reproduce.) Some organisms consist of a single cell and others are multicellular. Scientists classify cells as prokaryotic or eukaryotic. **Prokaryotes** are single-celled or colonial organisms that do not have membrane-bound nuclei. In contrast, the cells of **eukaryotes** do have membrane-bound organelles and a membrane-bound nucleus.

In larger organisms, cells combine to make **tissues**,

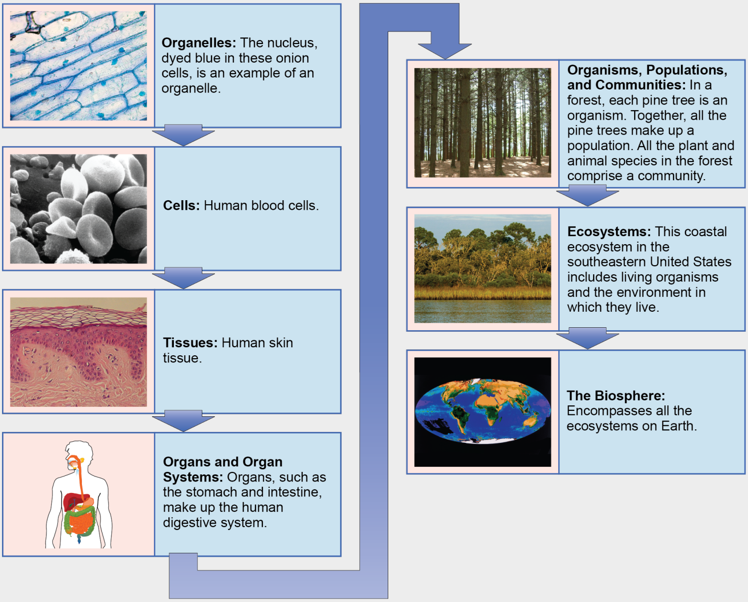
which are groups of similar cells carrying out similar or related functions. **Organs** are collections of tissues grouped together performing a common function. Organs are present not only in animals but also in plants. An **organ system** is a higher level of organization that consists of functionally related organs. Mammals have many organ systems. For instance, the circulatory system transports blood through the body and to and from the lungs. It includes organs such as the heart and blood vessels. **Organisms** are individual living entities. For example, each tree in a forest is an organism. Single-celled prokaryotes and single-celled eukaryotes are also organisms, which biologists typically call microorganisms.

Biologists collectively call all the individuals of a species living within a specific area a **population**. For example, a forest may include many pine trees, which represent the population of pine trees in this forest. Different populations may live in the same specific area. For example, the forest with the pine trees includes populations of flowering plants, insects, and microbial populations. A **community** is the sum of populations inhabiting a particular area. For instance, all of the trees, flowers, insects, and other populations in a forest form the forest's community. The forest itself is an ecosystem. An **ecosystem** consists of all the living things in a particular area together with the abiotic, nonliving parts of that environment such as nitrogen in the

soil or rain water. At the highest level of organization ([link]), the **biosphere** is the collection of all ecosystems, and it represents the zones of life on Earth. It includes land, water, and even the atmosphere to a certain extent.

Visual Connection

shows the biological levels of organization of living things. From a single organelle to the entire biosphere, living organisms are parts of a highly structured hierarchy. (credit “organelles”: modification of work by Umberto Salvagnin; credit “cells”: modification of work by Bruce Wetzel, Harry Schaefer/ National Cancer Institute; credit “tissues”: modification of work by Kilbad; Fama Clamosa; Mikael Häggström; credit “organs”: modification of work by Mariana Ruiz Villareal; credit “organisms”: modification of work by "Crystal"/Flickr; credit “ecosystems”: modification of work by US Fish and Wildlife Service Headquarters; credit “biosphere”: modification of work by NASA)



Which of the following statements is false?

1. Tissues exist within organs which exist within organ systems.
2. Communities exist within populations which exist within ecosystems.
3. Organelles exist within cells which exist within tissues.
4. Communities exist within ecosystems which exist in the biosphere.

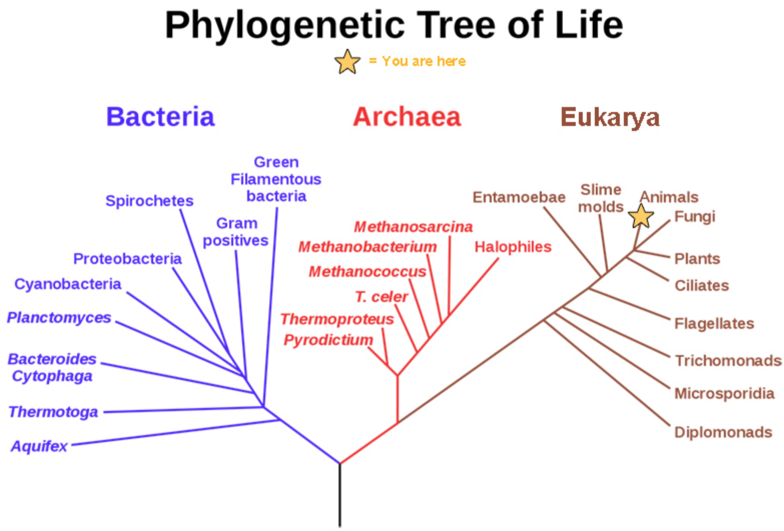
Microbiologist Carl Woese constructed this phylogenetic tree using data that he obtained from sequencing ribosomal RNA genes. The tree shows the separation of living organisms into three domains: Bacteria, Archaea, and Eukarya. Bacteria

and Archaea are prokaryotes, single-celled organisms lacking intracellular organelles. (credit: Eric Gaba; NASA Astrobiology Institute)

The Diversity of Life

The fact that biology, as a science, has such a broad scope has to do with the tremendous diversity of life on earth. The source of this diversity is **evolution**, the process of gradual change in a population or species over time. Evolutionary biologists study the evolution of living things in everything from the microscopic world to ecosystems.

A phylogenetic tree ([link]) can summarize the evolution of various life forms on Earth. It is a diagram showing the evolutionary relationships among biological species based on similarities and differences in genetic or physical traits or both. Nodes and branches comprise a phylogenetic tree. The internal nodes represent ancestors and are points in evolution when, based on scientific evidence, researchers believe an ancestor has diverged to form two new species. The length of each branch is proportional to the time elapsed since the split.



Evolution Connection

Carl Woese and the Phylogenetic Tree

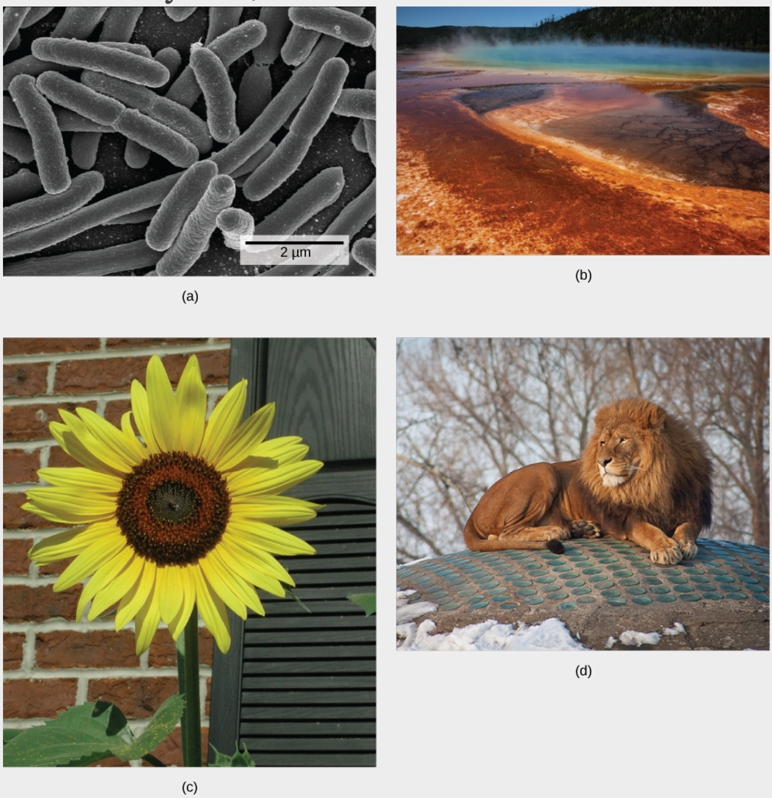
In the past, biologists grouped living organisms into five kingdoms: animals, plants, fungi, protists, and bacteria. They based the organizational scheme mainly on physical features, as opposed to physiology, biochemistry, or molecular biology, all of which modern systematics use. American microbiologist Carl Woese's pioneering work in the early 1970s has shown, however, that life on Earth has evolved along three lineages, now called domains—Bacteria, Archaea, and Eukarya. The first two are prokaryotic cells with microbes that lack membrane-enclosed nuclei and organelles. The third domain contains the eukaryotes and includes unicellular microorganisms (protists), together with

the three remaining kingdoms (fungi, plants, and animals). Woese defined Archaea as a new domain, and this resulted in a new taxonomic tree ([link]). Many organisms belonging to the Archaea domain live under extreme conditions and are called extremophiles. To construct his tree, Woese used genetic relationships rather than similarities based on morphology (shape).

Woese constructed his tree from universally distributed comparative gene sequencing that are present in every organism, and conserved (meaning that these genes have remained essentially unchanged throughout evolution). Woese's approach was revolutionary because comparing physical features are insufficient to differentiate between the prokaryotes that appear fairly similar in spite of their tremendous biochemical diversity and genetic variability ([link]). Comparing homologous DNA and RNA sequences provided Woese with a sensitive device that revealed the extensive variability of prokaryotes, and which justified separating the prokaryotes into two domains: bacteria and archaea.

These images represent different domains. The (a) bacteria in this micrograph belong to Domain Bacteria, while the (b) extremophiles (not visible) living in this hot vent belong to Domain Archaea. Both the (c) sunflower and (d) lion are part of Domain Eukarya. (credit a: modification of work by Drew March; credit b: modification of work by Steve Jurvetson; credit c: modification of work by

Michael Arrighi; credit d: modification of work by Leszek Leszcynski)



Researchers work on excavating dinosaur fossils at a site in Castellón, Spain. (credit: Mario Modesto)

Branches of Biological Study

The scope of biology is broad and therefore contains many branches and subdisciplines. Biologists may pursue one of those subdisciplines and work in a

more focused field. For instance, **molecular biology** and **biochemistry** study biological processes at the molecular and chemical level, including interactions among molecules such as DNA, RNA, and proteins, as well as the way they are regulated. **Microbiology**, the study of microorganisms, is the study of the structure and function of single-celled organisms. It is quite a broad branch itself, and depending on the subject of study, there are also microbial physiologists, ecologists, and geneticists, among others.

Career Connection

Forensic Scientist

Forensic science is the application of science to answer questions related to the law. Biologists as well as chemists and biochemists can be forensic scientists. Forensic scientists provide scientific evidence for use in courts, and their job involves examining trace materials associated with crimes. Interest in forensic science has increased in the last few years, possibly because of popular television shows that feature forensic scientists on the job. Also, developing molecular techniques and establishing DNA databases have expanded the types of work that forensic scientists can do. Their job activities are primarily related to crimes against people such as murder, rape, and assault. Their work involves analyzing samples such as hair,

blood, and other body fluids and also processing DNA ([link]) found in many different environments and materials. Forensic scientists also analyze other biological evidence left at crime scenes, such as insect larvae or pollen grains. Students who want to pursue careers in forensic science will most likely have to take chemistry and biology courses as well as some intensive math courses.

This forensic scientist works in a DNA extraction room at the U.S. Army Criminal Investigation Laboratory at Fort Gillem, GA. (credit: United States Army CID Command Public Affairs)

Another field of biological study, **neurobiology**, studies the biology of the nervous system, and although it is a branch of biology, it is also an interdisciplinary field of study known as

neuroscience. Because of its interdisciplinary nature, this subdiscipline studies different nervous system functions using molecular, cellular, developmental, medical, and computational approaches.

Paleontology, another branch of biology, uses fossils to study life's history ([link]). **Zoology** and **botany** are the study of animals and plants, respectively. Biologists can also specialize as biotechnologists, ecologists, or physiologists, to name just a few areas. This is just a small sample of the many fields that biologists can pursue.

Biology is the culmination of the achievements of the natural sciences from their inception to today. Excitingly, it is the cradle of emerging sciences, such as the biology of brain activity, genetic engineering of custom organisms, and the biology of evolution

that uses the laboratory tools of molecular biology to retrace the earliest stages of life on Earth. A scan of news headlines—whether reporting on immunizations, a newly discovered species, sports doping, or a genetically-modified food—demonstrates the way biology is active in and important to our everyday world.

Section Summary

Biology is the science of life. All living organisms share several key properties such as order, sensitivity or response to stimuli, reproduction, growth and development, regulation, homeostasis, and energy processing. Living things are highly organized parts of a hierarchy that includes atoms, molecules, organelles, cells, tissues, organs, and organ systems. In turn, biologists group organisms as populations, communities, ecosystems, and the biosphere. The great diversity of life today evolved from less-diverse ancestral organisms over billions of years. We can use a phylogenetic tree to show evolutionary relationships among organisms.

Biology is very broad and includes many branches and subdisciplines. Examples include molecular biology, microbiology, neurobiology, zoology, and botany, among others.

Visual Connection Questions

[link] Which of the following statements is false?

1. Tissues exist within organs which exist within organ systems.
2. Communities exist within populations which exist within ecosystems.
3. Organelles exist within cells which exist within tissues.
4. Communities exist within ecosystems which exist in the biosphere.

[link] Communities exist within populations which exist within ecosystems.

Review Questions

The smallest unit of biological structure that meets the functional requirements of "living" is the ______.

1. organ
2. organelle
3. cell

4. macromolecule

C

Viruses are not considered living because they ______.

1. are not made of cells
2. lack cell nuclei
3. do not contain DNA or RNA
4. cannot reproduce

A

The presence of a membrane-enclosed nucleus is a characteristic of ______.

1. prokaryotic cells
2. eukaryotic cells
3. living organisms
4. bacteria

B

A group of individuals of the same species living in the same area is called a(n) ______.

1. family
2. community
3. population
4. ecosystem

C

Which of the following sequences represents the hierarchy of biological organization from the most inclusive to the least complex level?

1. organelle, tissue, biosphere, ecosystem, population
2. organ, organism, tissue, organelle, molecule
3. organism, community, biosphere, molecule, tissue, organ
4. biosphere, ecosystem, community, population, organism

D

Where in a phylogenetic tree would you expect to find the organism that had evolved most recently?

1. at the base
2. within the branches

3. at the nodes
4. at the branch tips

D

Critical Thinking Questions

Select two items that biologists agree are necessary in order to consider an organism “alive.” For each, give an example of a nonliving object that otherwise fits the definition of “alive.”

Answers will vary. Layers of sedimentary rock have order but are not alive. Technology is capable of regulation but is not, of itself, alive.

Consider the levels of organization of the biological world, and place each of these items in order from smallest level of organization to most encompassing: skin cell, elephant, water molecule, planet Earth, tropical rainforest, hydrogen atom, wolf pack, liver.

Smallest level of organization to largest:

hydrogen atom, water molecule, skin cell, liver, elephant, wolf pack, tropical rainforest, planet Earth

You go for a long walk on a hot day. Give an example of a way in which homeostasis keeps your body healthy.

During your walk, you may begin to perspire, which cools your body and helps your body to maintain a constant internal temperature. You might also become thirsty and pause long enough for a cool drink, which will help to restore the water lost during perspiration.

Using examples, explain how biology can be studied from a microscopic approach to a global approach.

Researchers can approach biology from the smallest to the largest, and everything in between. For instance, an ecologist may study a population of individuals, the population's community, the community's ecosystem, and the ecosystem's part in the biosphere. When studying an individual organism, a biologist could examine the cell and its organelles, the tissues that the cells make up, the organs and

their respective organ systems, and the sum total—the organism itself.

Glossary

atom
: smallest and most fundamental unit of matter

biochemistry
: study of the chemistry of biological organisms

biosphere
: collection of all the ecosystems on Earth

botany
: study of plants

cell
: smallest fundamental unit of structure and function in living things

community
: set of populations inhabiting a particular area

ecosystem
: all the living things in a particular area together with the abiotic, nonliving parts of that environment

eukaryote
: organism with cells that have nuclei and

membrane-bound organelles

evolution
: the process of gradual change in a population or species over time

homeostasis
: ability of an organism to maintain constant internal conditions

macromolecule
: large molecule, typically formed by the joining of smaller molecules

microbiology
: study of the structure and function of microorganisms

molecule
: chemical structure consisting of at least two atoms held together by one or more chemical bonds

molecular biology
: study of biological processes and their regulation at the molecular level, including interactions among molecules such as DNA, RNA, and proteins

neurobiology
: study of the biology of the nervous system

organ

collection of related tissues grouped together performing a common function

organ system
: level of organization that consists of functionally related interacting organs

organelle
: small structures that exist within cells and carry out cellular functions

organism
: individual living entity

paleontology
: study of life's history by means of fossils

phylogenetic tree
: diagram showing the evolutionary relationships among various biological species based on similarities and differences in genetic or physical traits or both; in essence, a hypothesis concerning evolutionary connections

population
: all of the individuals of a species living within a specific area

prokaryote
: single-celled organism that lacks organelles and does not have nuclei surrounded by a

nuclear membrane

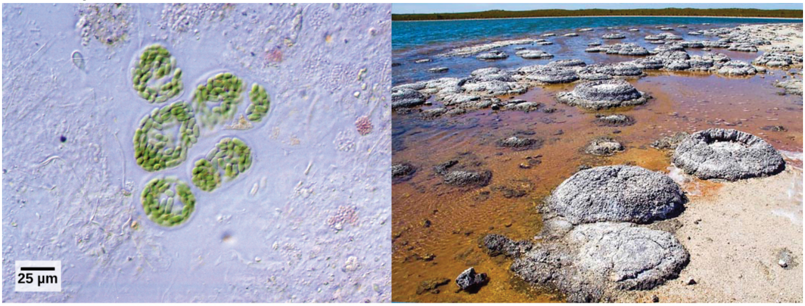
tissue
: group of similar cells carrying out related functions

zoology
: study of animals

The Process of Science
By the end of this section, you will be able to:

- Identify the shared characteristics of the natural sciences
- Understand the process of scientific inquiry
- Compare inductive reasoning with deductive reasoning
- Describe the goals of basic science and applied science

Formerly called blue-green algae, the (a) cyanobacteria seen through a light microscope are some of Earth’s oldest life forms. These (b) stromatolites along the shores of Lake Thetis in Western Australia are ancient structures formed by the layering of cyanobacteria in shallow waters. (credit a: modification of work by NASA; scale-bar data from Matt Russell; credit b: modification of work by Ruth Ellison)



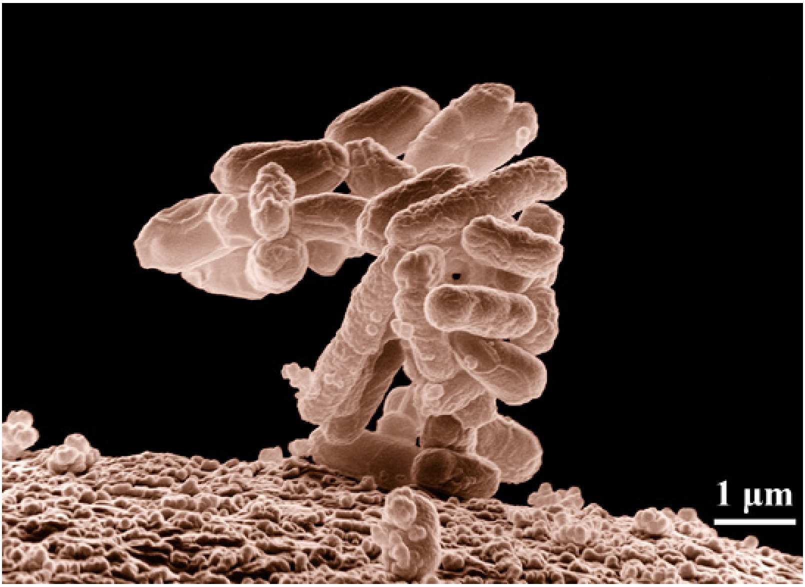
(a)

(b)

Like geology, physics, and chemistry, biology is a science that gathers knowledge about the natural

world. Specifically, biology is the study of life. The discoveries of biology are made by a community of researchers who work individually and together using agreed-on methods. In this sense, biology, like all sciences is a social enterprise like politics or the arts. The methods of science include careful observation, record keeping, logical and mathematical reasoning, experimentation, and submitting conclusions to the scrutiny of others. Science also requires considerable imagination and creativity; a well-designed experiment is commonly described as elegant, or beautiful. Like politics, science has considerable practical implications and some science is dedicated to practical applications, such as the prevention of disease (see [link]). Other science proceeds largely motivated by curiosity. Whatever its goal, there is no doubt that science, including biology, has transformed human existence and will continue to do so.

Biologists may choose to study *Escherichia coli* (*E. coli*), a bacterium that is a normal resident of our digestive tracts but which is also sometimes responsible for disease outbreaks. In this micrograph, the bacterium is visualized using a scanning electron microscope and digital colorization. (credit: Eric Erbe; digital colorization by Christopher Pooley, USDA-ARS)



Some fields of science include astronomy, biology, computer science, geology, logic, physics, chemistry, and mathematics. (credit: "Image Editor"/Flickr)

The Nature of Science

Biology is a science, but what exactly is science? What does the study of biology share with other scientific disciplines? **Science** (from the Latin *scientia,* meaning "knowledge") can be defined as knowledge about the natural world.

Science is a very specific way of learning, or knowing, about the world. The history of the past 500 years demonstrates that science is a very powerful way of knowing about the world; it is largely responsible for the technological revolutions that have taken place during this time. There are

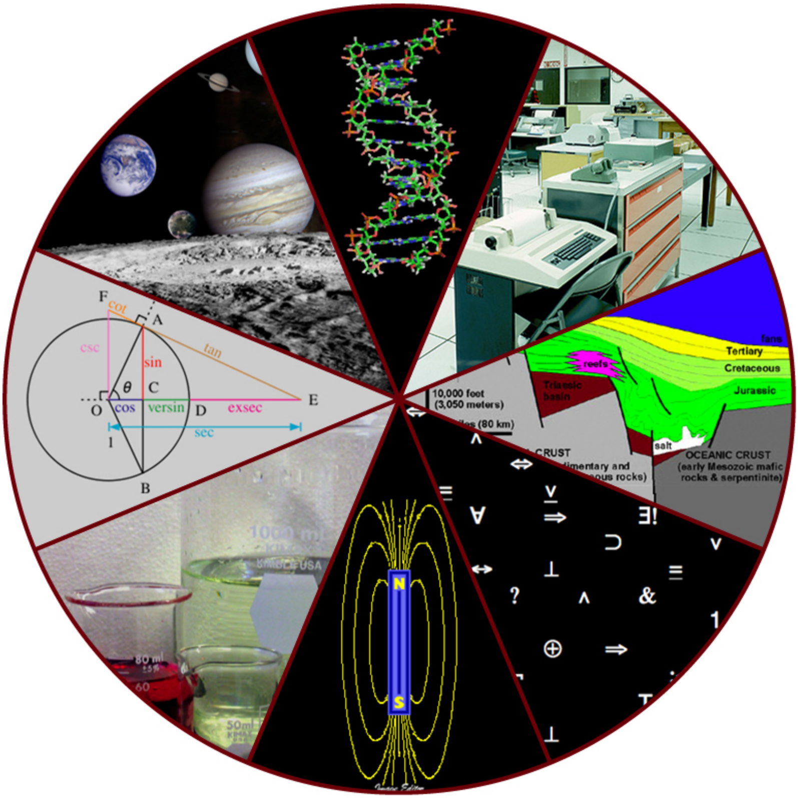
however, areas of knowledge and human experience that the methods of science cannot be applied to. These include such things as answering purely moral questions, aesthetic questions, or what can be generally categorized as spiritual questions. Science cannot investigate these areas because they are outside the realm of material phenomena, the phenomena of matter and energy, and cannot be observed and measured.

The **scientific method** is a method of research with defined steps that include experiments and careful observation. The steps of the scientific method will be examined in detail later, but one of the most important aspects of this method is the testing of hypotheses. A **hypothesis** is a suggested explanation for an event, which can be tested. Hypotheses, or tentative explanations, are generally produced within the context of a **scientific theory**. A scientific theory is a generally accepted, thoroughly tested and confirmed explanation for a set of observations or phenomena. Scientific theory is the foundation of scientific knowledge. In addition, in many scientific disciplines (less so in biology) there are **scientific laws**, often expressed in mathematical formulas, which describe how elements of nature will behave under certain specific conditions. There is not an evolution of hypotheses through theories to laws as if they represented some increase in certainty about the world. Hypotheses are the day-to-day material that

scientists work with and they are developed within the context of theories. Laws are concise descriptions of parts of the world that are amenable to formulaic or mathematical description.

Natural Sciences

What would you expect to see in a museum of natural sciences? Frogs? Plants? Dinosaur skeletons? Exhibits about how the brain functions? A planetarium? Gems and minerals? Or maybe all of the above? Science includes such diverse fields as astronomy, biology, computer sciences, geology, logic, physics, chemistry, and mathematics ([link]). However, those fields of science related to the physical world and its phenomena and processes are considered **natural sciences**. Thus, a museum of natural sciences might contain any of the items listed above.



There is no complete agreement when it comes to defining what the natural sciences include. For some experts, the natural sciences are astronomy, biology, chemistry, earth science, and physics. Other scholars choose to divide natural sciences into **life sciences**, which study living things and include biology, and **physical sciences**, which study nonliving matter and include astronomy, physics, and chemistry. Some disciplines such as biophysics and biochemistry build on two sciences and are interdisciplinary.

Scientific Inquiry

One thing is common to all forms of science: an ultimate goal "to know." Curiosity and inquiry are the driving forces for the development of science. Scientists seek to understand the world and the way it operates. Two methods of logical thinking are used: inductive reasoning and deductive reasoning.

Inductive reasoning is a form of logical thinking that uses related observations to arrive at a general conclusion. This type of reasoning is common in descriptive science. A life scientist such as a biologist makes observations and records them. These data can be qualitative (descriptive) or quantitative (consisting of numbers), and the raw data can be supplemented with drawings, pictures, photos, or videos. From many observations, the scientist can infer conclusions (inductions) based on evidence. Inductive reasoning involves formulating generalizations inferred from careful observation and the analysis of a large amount of data. Brain studies often work this way. Many brains are observed while people are doing a task. The part of the brain that lights up, indicating activity, is then demonstrated to be the part controlling the response to that task.

Deductive reasoning or deduction is the type of logic used in hypothesis-based science. In deductive reasoning, the pattern of thinking moves in the

opposite direction as compared to inductive reasoning. **Deductive reasoning** is a form of logical thinking that uses a general principle or law to forecast specific results. From those general principles, a scientist can extrapolate and predict the specific results that would be valid as long as the general principles are valid. For example, a prediction would be that if the climate is becoming warmer in a region, the distribution of plants and animals should change. Comparisons have been made between distributions in the past and the present, and the many changes that have been found are consistent with a warming climate. Finding the change in distribution is evidence that the climate change conclusion is a valid one.

Both types of logical thinking are related to the two main pathways of scientific study: descriptive science and hypothesis-based science. **Descriptive** (or discovery) **science** aims to observe, explore, and discover, while **hypothesis-based science** begins with a specific question or problem and a potential answer or solution that can be tested. The boundary between these two forms of study is often blurred, because most scientific endeavors combine both approaches. Observations lead to questions, questions lead to forming a hypothesis as a possible answer to those questions, and then the hypothesis is tested. Thus, descriptive science and hypothesis-based science are in continuous dialogue.

Sir Francis Bacon is credited with being the first to

document the scientific method.

Hypothesis Testing

Biologists study the living world by posing questions about it and seeking science-based responses. This approach is common to other sciences as well and is often referred to as the scientific method. The scientific method was used even in ancient times, but it was first documented by England's Sir Francis Bacon (1561–1626) ([link]), who set up inductive methods for scientific inquiry. The scientific method is not exclusively used by biologists but can be applied to almost anything as a logical problem-solving method.

The scientific process typically starts with an observation (often a problem to be solved) that leads to a question. Let’s think about a simple problem that starts with an observation and apply the scientific method to solve the problem. One Monday morning, a student arrives at class and quickly discovers that the classroom is too warm. That is an observation that also describes a problem: the classroom is too warm. The student then asks a question: “Why is the classroom so warm?”

Recall that a hypothesis is a suggested explanation that can be tested. To solve a problem, several hypotheses may be proposed. For example, one hypothesis might be, “The classroom is warm because no one turned on the air conditioning.” But there could be other responses to the question, and therefore other hypotheses may be proposed. A second hypothesis might be, “The classroom is warm because there is a power failure, and so the air conditioning doesn’t work.”

Once a hypothesis has been selected, a prediction may be made. A prediction is similar to a hypothesis but it typically has the format “If . . . then . . . .” For example, the prediction for the first hypothesis might be, “*If* the student turns on the air conditioning, *then* the classroom will no longer be too warm.”

A hypothesis must be testable to ensure that it is valid. For example, a hypothesis that depends on what a bear thinks is not testable, because it can never be known what a bear thinks. It should also be **falsifiable**, meaning that it can be disproven by experimental results. An example of an unfalsifiable hypothesis is “Botticelli’s *Birth of Venus* is beautiful.” There is no experiment that might show this statement to be false. To test a hypothesis, a researcher will conduct one or more experiments designed to eliminate one or more of the hypotheses. This is important. A hypothesis can be

disproven, or eliminated, but it can never be proven. Science does not deal in proofs like mathematics. If an experiment fails to disprove a hypothesis, then we find support for that explanation, but this is not to say that down the road a better explanation will not be found, or a more carefully designed experiment will be found to falsify the hypothesis.

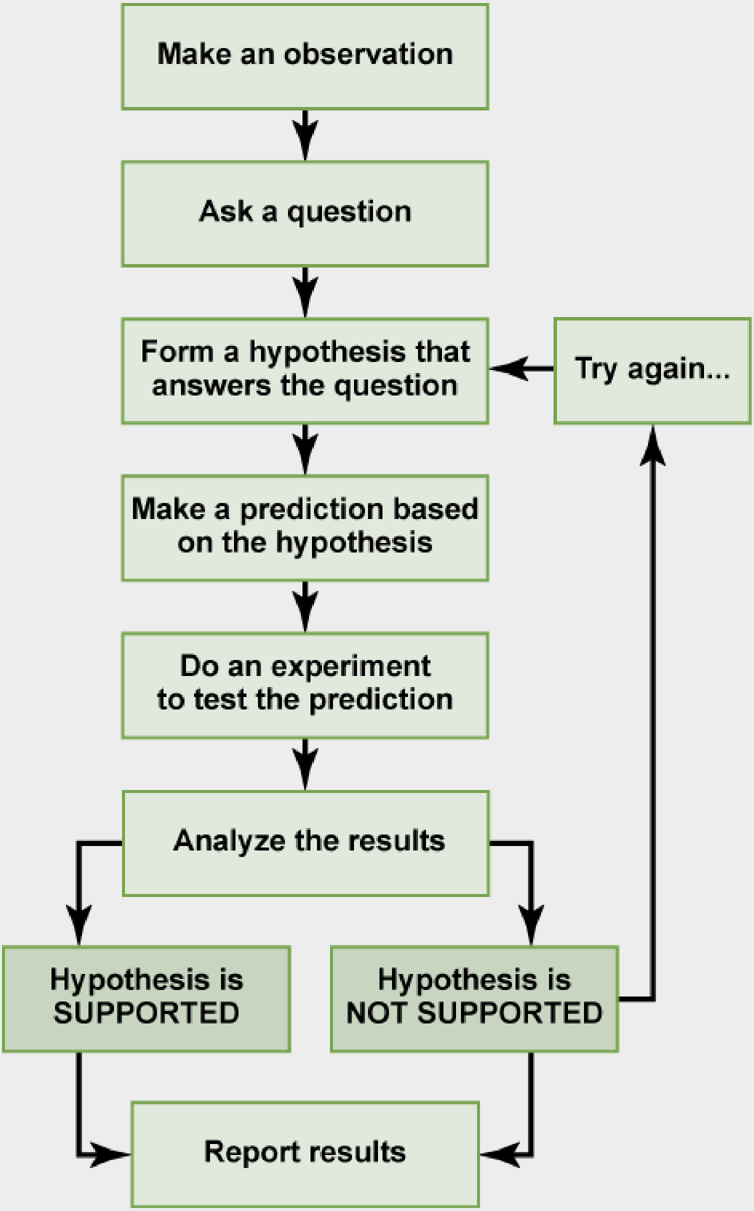
Each experiment will have one or more variables and one or more controls. A **variable** is any part of the experiment that can vary or change during the experiment. A **control** is a part of the experiment that does not change. Look for the variables and controls in the example that follows. As a simple example, an experiment might be conducted to test the hypothesis that phosphate limits the growth of algae in freshwater ponds. A series of artificial ponds are filled with water and half of them are treated by adding phosphate each week, while the other half are treated by adding a salt that is known not to be used by algae. The variable here is the phosphate (or lack of phosphate), the experimental or treatment cases are the ponds with added phosphate and the control ponds are those with something inert added, such as the salt. Just adding something is also a control against the possibility that adding extra matter to the pond has an effect. If the treated ponds show lesser growth of algae, then we have found support for our hypothesis. If they do not, then we reject our hypothesis. Be aware that rejecting one hypothesis does not determine

whether or not the other hypotheses can be accepted; it simply eliminates one hypothesis that is not valid ([link]). Using the scientific method, the hypotheses that are inconsistent with experimental data are rejected.

In recent years a new approach of testing hypotheses has developed as a result of an exponential growth of data deposited in various databases. Using computer algorithms and statistical analyses of data in databases, a new field of so-called "data research" (also referred to as "in silico" research) provides new methods of data analyses and their interpretation. This will increase the demand for specialists in both biology and computer science, a promising career opportunity.

Visual Connection

The scientific method is a series of defined steps that include experiments and careful observation. If a hypothesis is not supported by data, a new hypothesis can be proposed.



In the example below, the scientific method is used to solve an everyday problem. Which part in the example below is the hypothesis? Which is the prediction? Based on the results of the experiment,

is the hypothesis supported? If it is not supported, propose some alternative hypotheses.

1. My toaster doesn’t toast my bread.
2. Why doesn’t my toaster work?
3. There is something wrong with the electrical outlet.
4. If something is wrong with the outlet, my coffeemaker also won’t work when plugged into it.
5. I plug my coffeemaker into the outlet.
6. My coffeemaker works.

In practice, the scientific method is not as rigid and structured as it might at first appear. Sometimes an experiment leads to conclusions that favor a change in approach; often, an experiment brings entirely new scientific questions to the puzzle. Many times, science does not operate in a linear fashion; instead, scientists continually draw inferences and make generalizations, finding patterns as their research proceeds. Scientific reasoning is more complex than the scientific method alone suggests.

The Human Genome Project was a 13-year collaborative effort among researchers working in several different fields of science. The project was completed in 2003. (credit: the U.S. Department of Energy Genome Programs)

Basic and Applied Science

The scientific community has been debating for the last few decades about the value of different types of science. Is it valuable to pursue science for the sake of simply gaining knowledge, or does scientific knowledge only have worth if we can apply it to solving a specific problem or bettering our lives? This question focuses on the differences between two types of science: basic science and applied science.

Basic science or “pure” science seeks to expand knowledge regardless of the short-term application of that knowledge. It is not focused on developing a product or a service of immediate public or commercial value. The immediate goal of basic science is knowledge for knowledge’s sake, though this does not mean that in the end it may not result in an application.

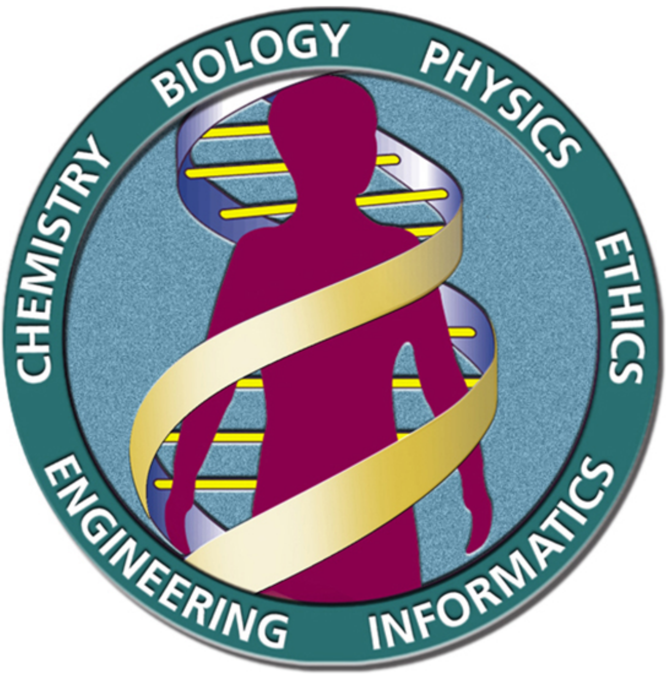
In contrast, **applied science** or “technology,” aims to use science to solve real-world problems, making it possible, for example, to improve a crop yield, find a cure for a particular disease, or save animals threatened by a natural disaster. In applied science, the problem is usually defined for the researcher.

Some individuals may perceive applied science as “useful” and basic science as “useless.” A question these people might pose to a scientist advocating

knowledge acquisition would be, “What for?” A careful look at the history of science, however, reveals that basic knowledge has resulted in many remarkable applications of great value. Many scientists think that a basic understanding of science is necessary before an application is developed; therefore, applied science relies on the results generated through basic science. Other scientists think that it is time to move on from basic science and instead to find solutions to actual problems. Both approaches are valid. It is true that there are problems that demand immediate attention; however, few solutions would be found without the help of the knowledge generated through basic science.

One example of how basic and applied science can work together to solve practical problems occurred after the discovery of DNA structure led to an understanding of the molecular mechanisms governing DNA replication. Strands of DNA, unique in every human, are found in our cells, where they provide the instructions necessary for life. During DNA replication, new copies of DNA are made, shortly before a cell divides to form new cells. Understanding the mechanisms of DNA replication enabled scientists to develop laboratory techniques that are now used to identify genetic diseases, pinpoint individuals who were at a crime scene, and determine paternity. Without basic science, it is unlikely that applied science would exist.

Another example of the link between basic and applied research is the Human Genome Project, a study in which each human chromosome was analyzed and mapped to determine the precise sequence of DNA subunits and the exact location of each gene. (The gene is the basic unit of heredity represented by a specific DNA segment that codes for a functional molecule.) Other organisms have also been studied as part of this project to gain a better understanding of human chromosomes. The Human Genome Project ([link]) relied on basic research carried out with non-human organisms and, later, with the human genome. An important end goal eventually became using the data for applied research seeking cures for genetically related diseases.



While research efforts in both basic science and applied science are usually carefully planned, it is important to note that some discoveries are made by serendipity, that is, by means of a fortunate accident or a lucky surprise. Penicillin was discovered when biologist Alexander Fleming accidentally left a petri dish of *Staphylococcus* bacteria open. An unwanted mold grew, killing the bacteria. The mold turned out to be *Penicillium*, and a new antibiotic was discovered. Even in the highly organized world of science, luck—when combined with an observant, curious mind—can lead to unexpected breakthroughs.

Reporting Scientific Work

Whether scientific research is basic science or applied science, scientists must share their findings for other researchers to expand and build upon their discoveries. Communication and collaboration within and between sub disciplines of science are key to the advancement of knowledge in science. For this reason, an important aspect of a scientist's work is disseminating results and communicating with peers. Scientists can share results by presenting them at a scientific meeting or conference, but this approach can reach only the limited few who are present. Instead, most scientists present their results in peer-reviewed articles that are published in scientific journals. **Peer-reviewed articles** are

scientific papers that are reviewed, usually anonymously by a scientist's colleagues, or peers. These colleagues are qualified individuals, often experts in the same research area, who judge whether or not the scientist's work is suitable for publication. The process of peer review helps to ensure that the research described in a scientific paper or grant proposal is original, significant, logical, and thorough. Grant proposals, which are requests for research funding, are also subject to peer review. Scientists publish their work so other scientists can reproduce their experiments under similar or different conditions to expand on the findings. The experimental results must be consistent with the findings of other scientists.

There are many journals and the popular press that do not use a peer-review system. A large number of online open-access journals, journals with articles available without cost, are now available many of which use rigorous peer-review systems, but some of which do not. Results of any studies published in these forums without peer review are not reliable and should not form the basis for other scientific work. In one exception, journals may allow a researcher to cite a personal communication from another researcher about unpublished results with the cited author's permission.

Section Summary

Biology is the science that studies living organisms and their interactions with one another and their environments. Science attempts to describe and understand the nature of the universe in whole or in part. Science has many fields; those fields related to the physical world and its phenomena are considered natural sciences.

A hypothesis is a tentative explanation for an observation. A scientific theory is a well-tested and consistently verified explanation for a set of observations or phenomena. A scientific law is a description, often in the form of a mathematical formula, of the behavior of an aspect of nature under certain circumstances. Two types of logical reasoning are used in science. Inductive reasoning uses results to produce general scientific principles. Deductive reasoning is a form of logical thinking that predicts results by applying general principles. The common thread throughout scientific research is the use of the scientific method. Scientists present their results in peer-reviewed scientific papers published in scientific journals.

Science can be basic or applied. The main goal of basic science is to expand knowledge without any expectation of short-term practical application of that knowledge. The primary goal of applied research, however, is to solve practical problems.

Art Connections

[link] In the example below, the scientific method is used to solve an everyday problem. Which part in the example below is the hypothesis? Which is the prediction? Based on the results of the experiment, is the hypothesis supported? If it is not supported, propose some alternative hypotheses.

1. My toaster doesn’t toast my bread.
2. Why doesn’t my toaster work?
3. There is something wrong with the electrical outlet.
4. If something is wrong with the outlet, my coffeemaker also won’t work when plugged into it.
5. I plug my coffeemaker into the outlet.
6. My coffeemaker works.

[link] The hypothesis is #3 (there is something wrong with the electrical outlet), and the prediction is #4 (if something is wrong with the outlet, then the coffeemaker also won’t work when plugged into the outlet). The original hypothesis is not supported, as the coffee maker works when plugged into the outlet. Alternative hypotheses may include (1) the toaster might be broken or (2) the toaster wasn’t turned on.

Multiple Choice

A suggested and testable explanation for an event is called a _____.

1. hypothesis
2. variable
3. theory
4. control

A

The type of logical thinking that uses related observations to arrive at a general conclusion is called _____.

1. deductive reasoning
2. the scientific method
3. hypothesis-based science
4. inductive reasoning

D

Free Response

Give an example of how applied science has had a direct effect on your daily life.

Answers will vary. One example of how applied science has had a direct effect on daily life is the presence of vaccines. Vaccines to prevent diseases such polio, measles, tetanus, and even the influenza affect daily life by contributing to individual and societal health.

Glossary

applied science
: a form of science that solves real-world problems

basic science
: science that seeks to expand knowledge regardless of the short-term application of that knowledge

control
: a part of an experiment that does not change during the experiment

deductive reasoning

a form of logical thinking that uses a general statement to forecast specific results

descriptive science
: a form of science that aims to observe, explore, and find things out

falsifiable
: able to be disproven by experimental results

hypothesis
: a suggested explanation for an event, which can be tested

hypothesis-based science
: a form of science that begins with a specific explanation that is then tested

inductive reasoning
: a form of logical thinking that uses related observations to arrive at a general conclusion

life science
: a field of science, such as biology, that studies living things

natural science
: a field of science that studies the physical world, its phenomena, and processes

peer-reviewed article
: a scientific report that is reviewed by a scientist's colleagues before publication

physical science

a field of science, such as astronomy, physics, and chemistry, that studies nonliving matter

science

knowledge that covers general truths or the operation of general laws, especially when acquired and tested by the scientific method

scientific law

a description, often in the form of a mathematical formula, for the behavior of some aspect of nature under certain specific conditions

scientific method

a method of research with defined steps that include experiments and careful observation

scientific theory

a thoroughly tested and confirmed explanation for observations or phenomena

variable

a part of an experiment that can vary or change

Atoms, Isotopes, Ions, and Molecules: The Building Blocks

By the end of this section, you will be able to do the following:

- Define matter and elements
- Describe the interrelationship between protons, neutrons, and electrons
- Compare the ways in which electrons can be donated or shared between atoms
- Explain the ways in which naturally occurring elements combine to create molecules, cells, tissues, organ systems, and organisms

At its most fundamental level, life is made up of matter. **Matter** is any substance that occupies space and has mass. **Elements** are unique forms of matter with specific chemical and physical properties that cannot break down into smaller substances by ordinary chemical reactions. There are 118 elements, but only 98 occur naturally. The remaining elements are unstable and require scientists to synthesize them in laboratories.

Each element is designated by its chemical symbol, which is a single capital letter or, when the first letter is already “taken” by another element, a combination of two letters. Some elements follow the English term for the element, such as C for carbon and Ca for calcium. Other elements’ chemical symbols derive from their Latin names. For

example, the symbol for sodium is Na, referring to *natrium*, the Latin word for sodium.

The four elements common to all living organisms are oxygen (O), carbon (C), hydrogen (H), and nitrogen (N). In the nonliving world, elements are found in different proportions, and some elements common to living organisms are relatively rare on the earth as a whole, as [link] shows. For example, the atmosphere is rich in nitrogen and oxygen but contains little carbon and hydrogen, while the earth's crust, although it contains oxygen and a small amount of hydrogen, has little nitrogen and carbon. In spite of their differences in abundance, all elements and the chemical reactions between them obey the same chemical and physical laws regardless of whether they are a part of the living or nonliving world.

Approximate Percentage of Elements in Living Organisms (Humans) Compared to the

Element	Life (Humans)	Atmosphere	Earth's Crust
			Nonliving World
Oxygen (O)	65%	21%	46%
Carbon (C)	18%	trace	trace
Hydrogen (H)	10%	trace	0.1%
Nitrogen (N)	3%	78%	trace

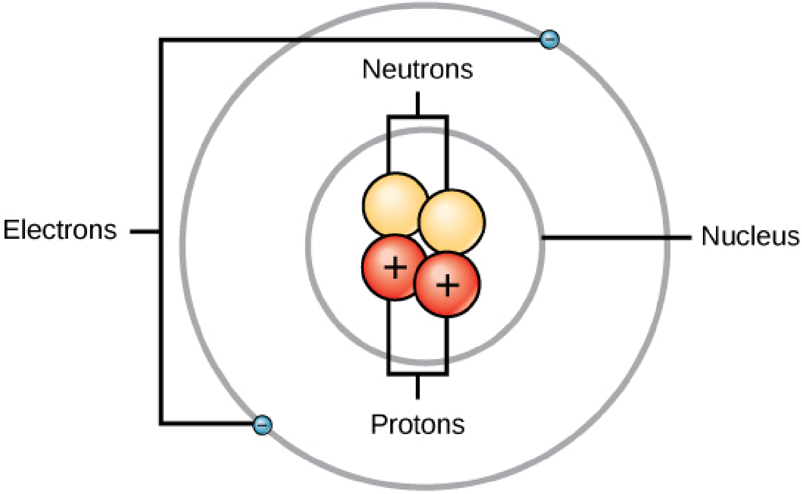
Elements, such as helium, depicted here, are made up of atoms. Atoms are made up of protons and neutrons located within the nucleus, with electrons in orbitals surrounding the nucleus.

The Structure of the Atom

To understand how elements come together, we must first discuss the element's smallest component or building block, the atom. An **atom** is the smallest unit of matter that retains all of the element's chemical properties. For example, one gold atom has all of the properties of gold in that it is a solid metal at room temperature. A gold coin is simply a very large number of gold atoms molded into the shape of a coin and contains small amounts of other elements known as impurities. We cannot break down gold atoms into anything smaller while still retaining the properties of gold.

An atom is composed of two regions: the **nucleus**,

which is in the atom's center and contains protons and neutrons. The atom's outermost region holds its electrons in orbit around the nucleus, as [link] illustrates. Atoms contain protons, electrons, and neutrons, among other subatomic particles. The only exception is hydrogen (H), which is made of one proton and one electron with no neutrons.



Protons and neutrons have approximately the same mass, about 1.67×10^{-24} grams. Scientists arbitrarily define this amount of mass as one atomic mass unit (amu) or one Dalton, as [link] shows. Although similar in mass, protons and neutrons differ in their electric charge. A **proton** is positively charged; whereas, a **neutron** is uncharged. Therefore, the number of neutrons in an atom contributes significantly to its mass, but not to its charge. **Electrons** are much smaller in mass than protons, weighing only 9.11×10^{-28} grams, or about 1/1800 of an atomic mass unit. Hence, they

do not contribute much to an element's overall atomic mass. Therefore, when considering atomic mass, it is customary to ignore the mass of any electrons and calculate the atom's mass based on the number of protons and neutrons alone. Although not significant contributors to mass, electrons do contribute greatly to the atom's charge, as each electron has a negative charge equal to the proton's positive charge. In uncharged, neutral atoms, the number of electrons orbiting the nucleus is equal to the number of protons inside the nucleus. In these atoms, the positive and negative charges cancel each other out, leading to an atom with no net charge.

Accounting for the sizes of protons, neutrons, and electrons, most of the atom's volume—greater than 99 percent—is empty space. With all this empty space, one might ask why so-called solid objects do not just pass through one another. The reason they do not is that the electrons that surround all atoms are negatively charged and negative charges repel each other.

Protons, Neutrons, and Electrons

	Charge	Mass (amu)	Location
Proton	+1	1	nucleus
Neutron	0	1	nucleus
Electron	–1	0	orbitals

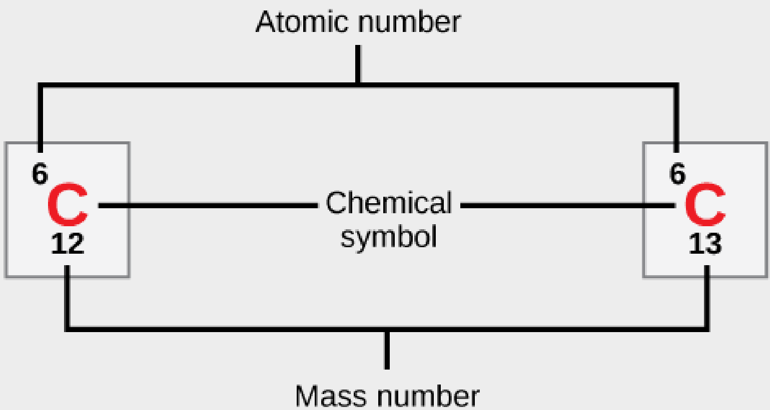
Atomic Number and Mass

Atoms of each element contain a characteristic number of protons and electrons. The number of protons determines an element's **atomic number**, which scientists use to distinguish one element from another. The number of neutrons is variable, resulting in isotopes, which are different forms of the same atom that vary only in the number of neutrons they possess. Together, the number of protons and neutrons determine an element's **mass number**, as [link] illustrates. Note that we disregard the small contribution of mass from electrons in calculating the mass number. We can use this approximation of mass to easily calculate how many neutrons an element has by simply subtracting the number of protons from the mass number. Since an element's isotopes will have slightly different mass numbers, scientists also determine the **atomic mass**, which is the calculated mean of the mass number for its naturally occurring isotopes. Often, the resulting number contains a fraction. For example, the atomic mass of chlorine (Cl) is 35.45 because chlorine is composed of several isotopes, some (the

majority) with atomic mass 35 (17 protons and 18 neutrons) and some with atomic mass 37 (17 protons and 20 neutrons).

Visual Connection

Carbon has an atomic number of six, and two stable isotopes with mass numbers of twelve and thirteen, respectively. Its relative atomic mass is 12.011



How many neutrons do carbon-12 and carbon-13 have, respectively?

Isotopes

Isotopes are different forms of an element that have the same number of protons but a different number

of neutrons. Some elements—such as carbon, potassium, and uranium—have naturally occurring isotopes. Carbon-12 contains six protons, six neutrons, and six electrons; therefore, it has a mass number of 12 (six protons and six neutrons). Carbon-14 contains six protons, eight neutrons, and six electrons; its atomic mass is 14 (six protons and eight neutrons). These two alternate forms of carbon are isotopes. Some isotopes may emit neutrons, protons, and electrons, and attain a more stable atomic configuration (lower level of potential energy); these are radioactive isotopes, or **radioisotopes**. Radioactive decay (carbon-14 decaying to eventually become nitrogen-14) describes the energy loss that occurs when an unstable atom's nucleus releases radiation.

Evolution Connection

Carbon Dating

Carbon is normally present in the atmosphere in the form of gaseous compounds like carbon dioxide and methane. Carbon-14 (^{14}C) is a naturally occurring radioisotope that is created in the atmosphere from atmospheric ^{14}N (nitrogen) by the addition of a neutron and the loss of a proton because of cosmic rays. This is a continuous process, so more ^{14}C is always being created. As a living organism incorporates ^{14}C initially as carbon dioxide fixed in the process of photosynthesis, the

relative amount of ^{14}C in its body is equal to the concentration of ^{14}C in the atmosphere. When an organism dies, it is no longer ingesting ^{14}C, so the ratio between ^{14}C and ^{12}C will decline as ^{14}C decays gradually to ^{14}N by a process called beta decay—electrons or positrons emission. This decay emits energy in a slow process.

After approximately 5,730 years, half of the starting concentration of ^{14}C will convert back to ^{14}N. We call the time it takes for half of the original concentration of an isotope to decay back to its more stable form its half-life. Because the half-life of ^{14}C is long, scientists use it to date formerly living objects such as old bones or wood. Comparing the ratio of the ^{14}C concentration in an object to the amount of ^{14}C in the atmosphere, scientists can determine the amount of the isotope that has not yet decayed. On the basis of this amount, [link] shows that we can calculate the age of the material, such as the pygmy mammoth, with accuracy if it is not much older than about 50,000 years. Other elements have isotopes with different half lives. For example, ^{40}K (potassium-40) has a half-life of 1.25 billion years, and ^{235}U (Uranium 235) has a half-life of about 700 million years. Through the use of radiometric dating, scientists can study the age of fossils or other remains of extinct organisms to understand how organisms have evolved from earlier species.

Scientists can determine the age of carbon-containing remains less than about 50,000 years

old, such as this pygmy mammoth, using carbon dating. (credit: Bill Faulkner, NPS)

Link to Learning

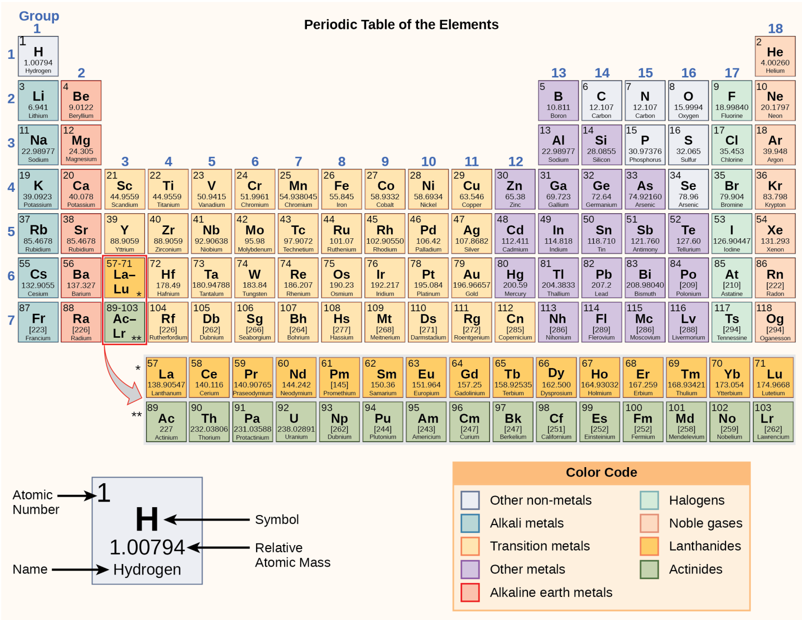
To learn more about atoms, isotopes, and how to tell one isotope from another, run the simulation. https://openstax.org/l/atoms_isotopes

The periodic table shows each element's atomic mass and atomic number. The atomic number appears above the symbol for the element and the approximate atomic mass appears below it.

The Periodic Table

The **periodic table** organizes and displays different elements. Devised by Russian chemist Dmitri Mendeleev (1834–1907) in 1869, the table groups elements that, although unique, share certain chemical properties with other elements. The properties of elements are responsible for their physical state at room temperature: they may be gases, solids, or liquids. Elements also have specific **chemical reactivity**, the ability to combine and to chemically bond with each other.

In the periodic table in [link], the elements are organized and displayed according to their atomic number and are arranged in a series of rows and columns based on shared chemical and physical properties. In addition to providing the atomic number for each element, the periodic table also displays the element's atomic mass. Looking at carbon, for example, its symbol (C) and name appear, as well as its atomic number of six (in the upper left-hand corner) and its atomic mass of 12.11.



The periodic table groups elements according to chemical properties. Scientists base the differences in chemical reactivity between the elements on the number and spatial distribution of an atom's electrons. Atoms that chemically react and bond to each other form molecules. **Molecules** are simply two or more atoms chemically bonded together. Logically, when two atoms chemically bond to form a molecule, their electrons, which form the outermost region of each atom, come together first as the atoms form a chemical bond.

Section Summary

Matter is anything that occupies space and has

mass. It is comprised of elements. All of the 98 elements that occur naturally have unique qualities that allow them to combine in various ways to create molecules, which in turn combine to form cells, tissues, organ systems, and organisms. Atoms, which consist of protons, neutrons, and electrons, are the smallest units of an element that retain all of the properties of that element. Electrons can transfer, share, or cause charge disparities between atoms to create bonds, including ionic, covalent, and hydrogen bonds, as well as van der Waals interactions.

Glossary

anion
: negative ion that is formed by an atom gaining one or more electrons

atom
: the smallest unit of matter that retains all of the chemical properties of an element

atomic mass
: calculated mean of the mass number for an element's isotopes

atomic number
: total number of protons in an atom

balanced chemical equation

statement of a chemical reaction with the number of each type of atom equalized for both the products and reactants

cation
: positive ion that is formed by an atom losing one or more electrons

chemical bond
: interaction between two or more of the same or different atoms that results in forming molecules

chemical reaction
: process leading to rearranging atoms in molecules

chemical reactivity
: the ability to combine and to chemically bond with each other

compound
: substance composed of molecules consisting of atoms of at least two different elements

covalent bond
: type of strong bond formed between two atoms of the same or different elements; forms when electrons are shared between atoms

electrolyte

ion necessary for nerve impulse conduction, muscle contractions, and water balance

electron
: negatively charged subatomic particle that resides outside of the nucleus in the electron orbital; lacks functional mass and has a negative charge of –1 unit

electron configuration
: arrangement of electrons in an atom's electron shell (for example, 1s22s22p6)

electron orbital
: how electrons are spatially distributed surrounding the nucleus; the area where we are most likely to find an electron

electron transfer
: movement of electrons from one element to another; important in creating ionic bonds

electronegativity
: ability of some elements to attract electrons (often of hydrogen atoms), acquiring partial negative charges in molecules and creating partial positive charges on the hydrogen atoms

element
: one of 118 unique substances that cannot break down into smaller substances; each

element has unique properties and a specified number of protons

equilibrium
: steady state of relative reactant and product concentration in reversible chemical reactions in a closed system

hydrogen bond
: weak bond between slightly positively charged hydrogen atoms and slightly negatively charged atoms in other molecules

inert gas
: (also, noble gas) element with filled outer electron shell that is unreactive with other atoms

ion
: atom or chemical group that does not contain equal numbers of protons and electrons

ionic bond
: chemical bond that forms between ions with opposite charges (cations and anions)

irreversible chemical reaction
: chemical reaction where reactants proceed unidirectionally to form products

isotope
: one or more forms of an element that have

different numbers of neutrons

law of mass action
: chemical law stating that the rate of a reaction is proportional to the concentration of the reacting substances

mass number
: total number of protons and neutrons in an atom

matter
: anything that has mass and occupies space

molecule
: two or more atoms chemically bonded together

neutron
: uncharged particle that resides in an atom's nucleus; has a mass of one amu

noble gas
: see inert gas

nonpolar covalent bond
: type of covalent bond that forms between atoms when electrons are shared equally between them

nucleus
: core of an atom; contains protons and neutrons

octet rule

rule that atoms are most stable when they hold eight electrons in their outermost shells

orbital

region surrounding the nucleus; contains electrons

periodic table

organizational chart of elements indicating each element's atomic number and atomic mass; provides key information about the elements' properties

polar covalent bond

type of covalent bond that forms as a result of unequal electron sharing, resulting in creating slightly positive and negative charged molecule regions

product

molecule that is result of chemical reaction

proton

positively charged particle that resides in the atom's nucleus; has a mass of one amu and a charge of $+1$

radioisotope

isotope that emits radiation comprised of subatomic particles to form more stable elements

reactant
: molecule that takes part in a chemical reaction

reversible chemical reaction
: chemical reaction that functions bidirectionally, where products may turn into reactants if their concentration is great enough

valence shell
: outermost shell of an atom

van der Waals interaction
: very weak interaction between molecules due to temporary charges attracting atoms that are very close together

Understanding Evolution

By the end of this section, you will be able to:

- Describe how the present-day theory of evolution was developed
- Define adaptation
- Explain convergent and divergent evolution
- Describe homologous and vestigial structures
- Discuss misconceptions about the theory of evolution

Evolution by natural selection describes a mechanism for how species change over time. That species change had been suggested and debated well before Darwin began to explore this idea. The view that species were static and unchanging was grounded in the writings of Plato, yet there were also ancient Greeks who expressed evolutionary ideas. In the eighteenth century, ideas about the evolution of animals were reintroduced by the naturalist Georges-Louis Leclerc Comte de Buffon who observed that various geographic regions have different plant and animal populations, even when the environments are similar. It was also accepted that there were extinct species.

During this time, James Hutton, a Scottish naturalist, proposed that geological change occurred gradually by the accumulation of small changes from processes operating like they are today over long periods of time. This contrasted with the

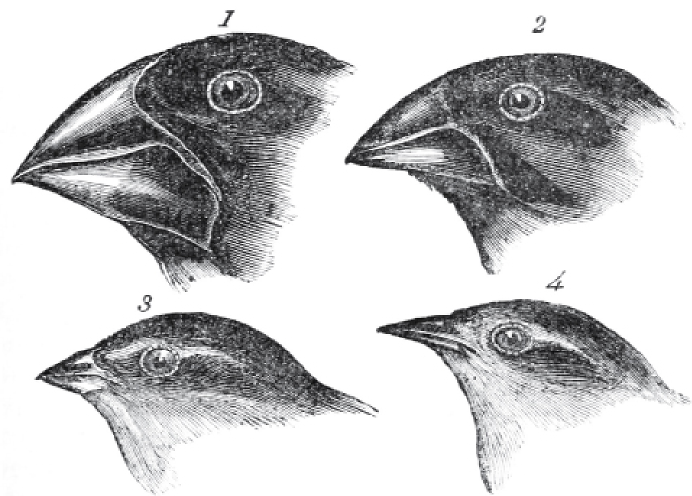
predominant view that the geology of the planet was a consequence of catastrophic events occurring during a relatively brief past. Hutton's view was popularized in the nineteenth century by the geologist Charles Lyell who became a friend to Darwin. Lyell's ideas were influential on Darwin's thinking: Lyell's notion of the greater age of Earth gave more time for gradual change in species, and the process of change provided an analogy for gradual change in species. In the early nineteenth century, Jean-Baptiste Lamarck published a book that detailed a mechanism for evolutionary change. This mechanism is now referred to as an inheritance of acquired characteristics by which modifications in an individual are caused by its environment, or the use or disuse of a structure during its lifetime, could be inherited by its offspring and thus bring about change in a species. While this mechanism for evolutionary change was discredited, Lamarck's ideas were an important influence on evolutionary thought.

Darwin observed that beak shape varies among finch species. He postulated that the beak of an ancestral species had adapted over time to equip the finches to acquire different food sources.Both (a) Charles Darwin and (b) Alfred Wallace wrote scientific papers on natural selection that were presented together before the Linnean Society in 1858.

Charles Darwin and Natural Selection

In the mid-nineteenth century, the actual mechanism for evolution was independently conceived of and described by two naturalists: Charles Darwin and Alfred Russel Wallace. Importantly, each naturalist spent time exploring the natural world on expeditions to the tropics. From 1831 to 1836, Darwin traveled around the world on *H.M.S. Beagle*, including stops in South America, Australia, and the southern tip of Africa. Wallace traveled to Brazil to collect insects in the Amazon rainforest from 1848 to 1852 and to the Malay Archipelago from 1854 to 1862. Darwin's journey, like Wallace's later journeys to the Malay Archipelago, included stops at several island chains, the last being the Galápagos Islands west of Ecuador. On these islands, Darwin observed species of organisms on different islands that were clearly similar, yet had distinct differences. For example, the ground finches inhabiting the Galápagos Islands comprised several species with a unique beak shape ([link]). The species on the islands had a graded series of beak sizes and shapes with very small differences between the most similar. He observed that these finches closely resembled another finch species on the mainland of South America. Darwin imagined that the island species might be species modified from one of the original mainland species. Upon further study, he realized that the varied beaks of each finch helped the birds acquire a specific type of food. For example, seed-eating finches had stronger, thicker beaks for breaking

seeds, and insect-eating finches had spear-like beaks for stabbing their prey.



1. Geospiza magnirostris
2. Geospiza fortis
3. Geospiza parvula
4. Certhidea olivacea

Finches from Galapagos Archipelago

Wallace and Darwin both observed similar patterns in other organisms and they independently developed the same explanation for how and why such changes could take place. Darwin called this mechanism natural selection. **Natural selection**, also known as “survival of the fittest,” is the more prolific reproduction of individuals with favorable traits that survive environmental change because of those traits; this leads to evolutionary change.

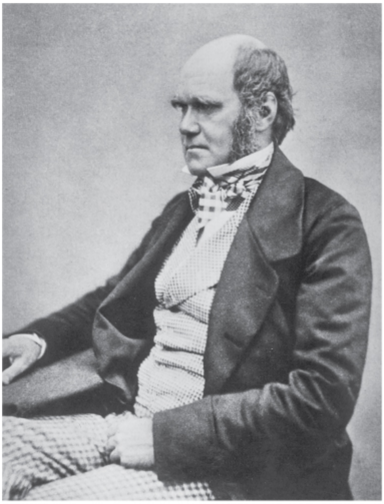
For example, a population of giant tortoises found in the Galapagos Archipelago was observed by Darwin to have longer necks than those that lived on other

islands with dry lowlands. These tortoises were "selected" because they could reach more leaves and access more food than those with short necks. In times of drought when fewer leaves would be available, those that could reach more leaves had a better chance to eat and survive than those that couldn't reach the food source. Consequently, long-necked tortoises would be more likely to be reproductively successful and pass the long-necked trait to their offspring. Over time, only long-necked tortoises would be present in the population.

Natural selection, Darwin argued, was an inevitable outcome of three principles that operated in nature. First, most characteristics of organisms are inherited, or passed from parent to offspring. Although no one, including Darwin and Wallace, knew how this happened at the time, it was a common understanding. Second, more offspring are produced than are able to survive, so resources for survival and reproduction are limited. The capacity for reproduction in all organisms outstrips the availability of resources to support their numbers. Thus, there is competition for those resources in each generation. Both Darwin and Wallace's understanding of this principle came from reading an essay by the economist Thomas Malthus who discussed this principle in relation to human populations. Third, offspring vary among each other in regard to their characteristics and those variations are inherited. Darwin and Wallace

reasoned that offspring with inherited characteristics which allow them to best compete for limited resources will survive and have more offspring than those individuals with variations that are less able to compete. Because characteristics are inherited, these traits will be better represented in the next generation. This will lead to change in populations over generations in a process that Darwin called descent with modification. Ultimately, natural selection leads to greater adaptation of the population to its local environment; it is the only mechanism known for adaptive evolution.

Papers by Darwin and Wallace ([link]) presenting the idea of natural selection were read together in 1858 before the Linnean Society in London. The following year Darwin's book, *On the Origin of Species,* was published. His book outlined in considerable detail his arguments for evolution by natural selection.



(a)

(b)

Demonstrations of evolution by natural selection are time consuming and difficult to obtain. One of the best examples has been demonstrated in the very birds that helped to inspire Darwin’s theory: the Galápagos finches. Peter and Rosemary Grant and their colleagues have studied Galápagos finch populations every year since 1976 and have provided important demonstrations of natural selection. The Grants found changes from one generation to the next in the distribution of beak shapes with the medium ground finch on the Galápagos island of Daphne Major. The birds have inherited variation in the bill shape with some birds having wide deep bills and others having thinner bills. During a period in which rainfall was higher than normal because of an El Niño, the large hard seeds that large-billed birds ate were reduced in number; however, there was an abundance of the

small soft seeds which the small-billed birds ate. Therefore, survival and reproduction were much better in the following years for the small-billed birds. In the years following this El Niño, the Grants measured beak sizes in the population and found that the average bill size was smaller. Since bill size is an inherited trait, parents with smaller bills had more offspring and the size of bills had evolved to be smaller. As conditions improved in 1987 and larger seeds became more available, the trend toward smaller average bill size ceased.

Career Connection

Field Biologist

Many people hike, explore caves, scuba dive, or climb mountains for recreation. People often participate in these activities hoping to see wildlife. Experiencing the outdoors can be incredibly enjoyable and invigorating. What if your job was to be outside in the wilderness? Field biologists by definition work outdoors in the "field." The term field in this case refers to any location outdoors, even under water. A field biologist typically focuses research on a certain species, group of organisms, or a single habitat ([link]).

A field biologist tranquilizes a polar bear for study. (credit: Karen Rhode)

One objective of many field biologists includes discovering new species that have never been recorded. Not only do such findings expand our understanding of the natural world, but they also lead to important innovations in fields such as medicine and agriculture. Plant and microbial species, in particular, can reveal new medicinal and nutritive knowledge. Other organisms can play key roles in ecosystems or be considered rare and in need of protection. When discovered, these important species can be used as evidence for environmental regulations and laws.

Flowering plants evolved from a common ancestor. Notice that the (a) dense blazing star (*Liatrus spicata*) and the (b) purple coneflower (*Echinacea*

purpurea) vary in appearance, yet both share a similar basic morphology. (credit a: modification of work by Drew Avery; credit b: modification of work by Cory Zanker)

Processes and Patterns of Evolution

Natural selection can only take place if there is **variation**, or differences, among individuals in a population. Importantly, these differences must have some genetic basis; otherwise, the selection will not lead to change in the next generation. This is critical because variation among individuals can be caused by non-genetic reasons such as an individual being taller because of better nutrition rather than different genes.

Genetic diversity in a population comes from two main mechanisms: mutation and sexual reproduction. Mutation, a change in DNA, is the ultimate source of new alleles, or new genetic variation in any population. The genetic changes caused by mutation can have one of three outcomes on the phenotype. A mutation affects the phenotype of the organism in a way that gives it reduced fitness—lower likelihood of survival or fewer offspring. A mutation may produce a phenotype with a beneficial effect on fitness. And, many mutations will also have no effect on the fitness of the phenotype; these are called neutral mutations. Mutations may also have a whole range of effect

sizes on the fitness of the organism that expresses them in their phenotype, from a small effect to a great effect. Sexual reproduction also leads to genetic diversity: when two parents reproduce, unique combinations of alleles assemble to produce the unique genotypes and thus phenotypes in each of the offspring.

A heritable trait that helps the survival and reproduction of an organism in its present environment is called an **adaptation**. Scientists describe groups of organisms becoming adapted to their environment when a change in the range of genetic variation occurs over time that increases or maintains the “fit” of the population to its environment. The webbed feet of platypuses are an adaptation for swimming. The snow leopards’ thick fur is an adaptation for living in the cold. The cheetahs’ fast speed is an adaptation for catching prey.

Whether or not a trait is favorable depends on the environmental conditions at the time. The same traits are not always selected because environmental conditions can change. For example, consider a species of plant that grew in a moist climate and did not need to conserve water. Large leaves were selected because they allowed the plant to obtain more energy from the sun. Large leaves require more water to maintain than small leaves, and the moist environment provided favorable conditions to

support large leaves. After thousands of years, the climate changed, and the area no longer had excess water. The direction of natural selection shifted so that plants with small leaves were selected because those populations were able to conserve water to survive the new environmental conditions.

The evolution of species has resulted in enormous variation in form and function. Sometimes, evolution gives rise to groups of organisms that become tremendously different from each other. When two species evolve in diverse directions from a common point, it is called **divergent evolution**. Such divergent evolution can be seen in the forms of the reproductive organs of flowering plants which share the same basic anatomies; however, they can look very different as a result of selection in different physical environments and adaptation to different kinds of pollinators ([link]).

In other cases, similar phenotypes evolve independently in distantly related species. For example, flight has evolved in both bats and insects,

and they both have structures we refer to as wings, which are adaptations to flight. However, the wings of bats and insects have evolved from very different original structures. This phenomenon is called **convergent evolution** , where similar traits evolve independently in species that do not share a common ancestry. The two species came to the same function, flying, but did so separately from each other.

These physical changes occur over enormous spans of time and help explain how evolution occurs. Natural selection acts on individual organisms, which in turn can shape an entire species. Although natural selection may work in a single generation on an individual, it can take thousands or even millions of years for the genotype of an entire species to evolve. It is over these large time spans that life on earth has changed and continues to change.

In this (a) display, fossil hominids are arranged from oldest (bottom) to newest (top). As hominids evolved, the shape of the skull changed. An artist's rendition of (b) extinct species of the genus *Equus* reveals that these ancient species resembled the modern horse (*Equus ferus*) but varied in size. The similar construction of these appendages indicates that these organisms share a common ancestor. The white winter coat of the (a) arctic fox and the (b) ptarmigan's plumage are adaptations to their environments. (credit a: modification of work by Keith Morehouse)

Evidence of Evolution

The evidence for evolution is compelling and extensive. Looking at every level of organization in living systems, biologists see the signature of past and present evolution. Darwin dedicated a large portion of his book, *On the Origin of Species*, to identifying patterns in nature that were consistent with evolution, and since Darwin, our understanding has become clearer and broader.

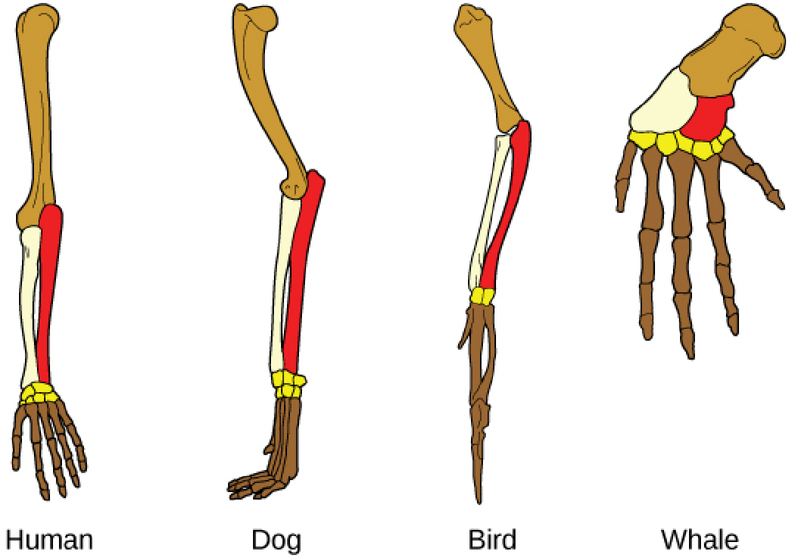
Fossils

Fossils provide solid evidence that organisms from the past are not the same as those found today, and fossils show a progression of evolution. Scientists determine the age of fossils and categorize them from all over the world to determine when the organisms lived relative to each other. The resulting fossil record tells the story of the past and shows the evolution of form over millions of years ([link]). For example, scientists have recovered highly detailed records showing the evolution of humans and horses ([link]). The whale flipper shares a similar morphology to appendages of birds and mammals ([link]) indicating that these species share a common ancestor.

(a) (b)

Anatomy and Embryology

Another type of evidence for evolution is the presence of structures in organisms that share the same basic form. For example, the bones in the appendages of a human, dog, bird, and whale all share the same overall construction ([link]) resulting from their origin in the appendages of a common ancestor. Over time, evolution led to changes in the shapes and sizes of these bones in different species, but they have maintained the same overall layout. Scientists call these synonymous parts **homologous structures**.



Some structures exist in organisms that have no apparent function at all, and appear to be residual parts from a past common ancestor. These unused structures without function are called **vestigial structures**. Other examples of vestigial structures are wings on flightless birds, leaves on some cacti, and hind leg bones in whales.

Link to Learning

Visit this interactive site to guess which bones structures are homologous and which are analogous, and see examples of evolutionary adaptations to illustrate these concepts.

Another evidence of evolution is the convergence of form in organisms that share similar environments. For example, species of unrelated animals, such as the arctic fox and ptarmigan, living in the arctic region have been selected for seasonal white phenotypes during winter to blend with the snow and ice ([link]**ab**). These similarities occur not because of common ancestry, but because of similar selection pressures—the benefits of not being seen by predators.

(a) (b)

Embryology, the study of the development of the anatomy of an organism to its adult form, also

provides evidence of relatedness between now widely divergent groups of organisms. Mutational tweaking in the embryo can have such magnified consequences in the adult that embryo formation tends to be conserved. As a result, structures that are absent in some groups often appear in their embryonic forms and disappear by the time the adult or juvenile form is reached. For example, all vertebrate embryos, including humans, exhibit gill slits and tails at some point in their early development. These disappear in the adults of terrestrial groups but are maintained in adult forms of aquatic groups such as fish and some amphibians. Great ape embryos, including humans, have a tail structure during their development that is lost by the time of birth.

Biogeography

The geographic distribution of organisms on the planet follows patterns that are best explained by evolution in conjunction with the movement of tectonic plates over geological time. Broad groups that evolved before the breakup of the supercontinent Pangaea (about 200 million years ago) are distributed worldwide. Groups that evolved since the breakup appear uniquely in regions of the planet, such as the unique flora and fauna of northern continents that formed from the supercontinent Laurasia and of the southern continents that formed from the supercontinent

Gondwana. The presence of members of the plant family Proteaceae in Australia, southern Africa, and South America is best by their presence prior to the southern supercontinent Gondwana breaking up.

The great diversification of marsupials in Australia and the absence of other mammals reflect Australia's long isolation. Australia has an abundance of endemic species—species found nowhere else—which is typical of islands whose isolation by expanses of water prevents species to migrate. Over time, these species diverge evolutionarily into new species that look very different from their ancestors that may exist on the mainland. The marsupials of Australia, the finches on the Galápagos, and many species on the Hawaiian Islands are all unique to their one point of origin, yet they display distant relationships to ancestral species on mainlands.

Molecular Biology

Like anatomical structures, the structures of the molecules of life reflect descent with modification. Evidence of a common ancestor for all of life is reflected in the universality of DNA as the genetic material and in the near universality of the genetic code and the machinery of DNA replication and expression. Fundamental divisions in life between the three domains are reflected in major structural differences in otherwise conservative structures such

as the components of ribosomes and the structures of membranes. In general, the relatedness of groups of organisms is reflected in the similarity of their DNA sequences—exactly the pattern that would be expected from descent and diversification from a common ancestor.

DNA sequences have also shed light on some of the mechanisms of evolution. For example, it is clear that the evolution of new functions for proteins commonly occurs after gene duplication events that allow the free modification of one copy by mutation, selection, or drift (changes in a population's gene pool resulting from chance), while the second copy continues to produce a functional protein.

Misconceptions of Evolution

Although the theory of evolution generated some controversy when it was first proposed, it was almost universally accepted by biologists, particularly younger biologists, within 20 years after publication of *On the Origin of Species*. Nevertheless, the theory of evolution is a difficult concept and misconceptions about how it works abound.

Link to Learning

This site addresses some of the main misconceptions associated with the theory of evolution.

Evolution Is Just a Theory

Critics of the theory of evolution dismiss its importance by purposefully confounding the everyday usage of the word “theory” with the way scientists use the word. In science, a “theory” is understood to be a body of thoroughly tested and verified explanations for a set of observations of the natural world. Scientists have a theory of the atom, a theory of gravity, and the theory of relativity, each of which describes understood facts about the world. In the same way, the theory of evolution describes facts about the living world. As such, a theory in science has survived significant efforts to discredit it by scientists. In contrast, a “theory” in common vernacular is a word meaning a guess or suggested explanation; this meaning is more akin to the scientific concept of “hypothesis.” When critics

of evolution say evolution is “just a theory,” they are implying that there is little evidence supporting it and that it is still in the process of being rigorously tested. This is a mischaracterization.

Individuals Evolve

Evolution is the change in genetic composition of a population over time, specifically over generations, resulting from differential reproduction of individuals with certain alleles. Individuals do change over their lifetime, obviously, but this is called development and involves changes programmed by the set of genes the individual acquired at birth in coordination with the individual’s environment. When thinking about the evolution of a characteristic, it is probably best to think about the change of the average value of the characteristic in the population over time. For example, when natural selection leads to bill-size change in medium-ground finches in the Galápagos, this does not mean that individual bills on the finches are changing. If one measures the average bill size among all individuals in the population at one time and then measures the average bill size in the population several years later, this average value will be different as a result of evolution. Although some individuals may survive from the first time to the second, they will still have the same bill size; however, there will be many new individuals that contribute to the shift in average bill size.

Evolution Explains the Origin of Life

It is a common misunderstanding that evolution includes an explanation of life's origins. Conversely, some of the theory's critics believe that it cannot explain the origin of life. The theory does not try to explain the origin of life. The theory of evolution explains how populations change over time and how life diversifies the origin of species. It does not shed light on the beginnings of life including the origins of the first cells, which is how life is defined. The mechanisms of the origin of life on Earth are a particularly difficult problem because it occurred a very long time ago, and presumably it just occurred once. Importantly, biologists believe that the presence of life on Earth precludes the possibility that the events that led to life on Earth can be repeated because the intermediate stages would immediately become food for existing living things.

However, once a mechanism of inheritance was in place in the form of a molecule like DNA either within a cell or pre-cell, these entities would be subject to the principle of natural selection. More effective reproducers would increase in frequency at the expense of inefficient reproducers. So while evolution does not explain the origin of life, it may have something to say about some of the processes operating once pre-living entities acquired certain properties.

Organisms Evolve on Purpose

Statements such as “organisms evolve in response to a change in an environment” are quite common, but such statements can lead to two types of misunderstandings. First, the statement must not be understood to mean that individual organisms evolve. The statement is shorthand for “a population evolves in response to a changing environment.” However, a second misunderstanding may arise by interpreting the statement to mean that the evolution is somehow intentional. A changed environment results in some individuals in the population, those with particular phenotypes, benefiting and therefore producing proportionately more offspring than other phenotypes. This results in change in the population if the characteristics are genetically determined.

It is also important to understand that the variation that natural selection works on is already in a population and does not arise in response to an environmental change. For example, applying antibiotics to a population of bacteria will, over time, select a population of bacteria that are resistant to antibiotics. The resistance, which is caused by a gene, did not arise by mutation because of the application of the antibiotic. The gene for resistance was already present in the gene pool of the bacteria, likely at a low frequency. The antibiotic, which kills the bacterial cells without the

resistance gene, strongly selects individuals that are resistant, since these would be the only ones that survived and divided. Experiments have demonstrated that mutations for antibiotic resistance do not arise as a result of antibiotic.

In a larger sense, evolution is not goal directed. Species do not become "better" over time; they simply track their changing environment with adaptations that maximize their reproduction in a particular environment at a particular time. Evolution has no goal of making faster, bigger, more complex, or even smarter species, despite the commonness of this kind of language in popular discourse. What characteristics evolve in a species are a function of the variation present and the environment, both of which are constantly changing in a non-directional way. What trait is fit in one environment at one time may well be fatal at some point in the future. This holds equally well for a species of insect as it does the human species.

Section Summary

Evolution is the process of adaptation through mutation which allows more desirable characteristics to be passed to the next generation. Over time, organisms evolve more characteristics that are beneficial to their survival. For living organisms to adapt and change to environmental

pressures, genetic variation must be present. With genetic variation, individuals have differences in form and function that allow some to survive certain conditions better than others. These organisms pass their favorable traits to their offspring. Eventually, environments change, and what was once a desirable, advantageous trait may become an undesirable trait and organisms may further evolve. Evolution may be convergent with similar traits evolving in multiple species or divergent with diverse traits evolving in multiple species that came from a common ancestor. Evidence of evolution can be observed by means of DNA code and the fossil record, and also by the existence of homologous and vestigial structures.

Review Questions

Which scientific concept did Charles Darwin and Alfred Wallace independently discover?

1. mutation
2. natural selection
3. overbreeding
4. sexual reproduction

B

Which of the following situations will lead to natural selection?

1. The seeds of two plants land near each other and one grows larger than the other.
2. Two types of fish eat the same kind of food, and one is better able to gather food than the other.
3. Male lions compete for the right to mate with females, with only one possible winner.
4. all of the above

D

Which description is an example of a phenotype?

1. A certain duck has a blue beak.
2. A mutation occurred to a flower.
3. Most cheetahs live solitary lives.
4. both a and c

D

Which situation is most likely an example of convergent evolution?

1. Squid and humans have eyes similar in structure.
2. Worms and snakes both move without legs.
3. Some bats and birds have wings that allow them to fly
4. all of the above

D

Free Response

If a person scatters a handful of garden pea plant seeds in one area, how would natural selection work in this situation?

The plants that can best use the resources of the area, including competing with other individuals for those resources will produce more seeds themselves and those traits that allowed them to better use the resources will increase in the population of the next generation.

Why do scientists consider vestigial structures evidence for evolution?

Vestigial structures are considered evidence for evolution because most structures do not exist in an organism without serving some function either presently or in the past. A vestigial structure indicates a past form or function that has since changed, but the structure remains present because it had a function in the ancestor.

How does the scientific meaning of “theory” differ from the common vernacular meaning?

In science, a theory is a thoroughly tested and verified set of explanations for a body of observations of nature. It is the strongest form of knowledge in science. In contrast, a theory in common vernacular can mean a guess or speculation about something, meaning that the knowledge implied by the theory is very weak.

Explain why the statement that a monkey is more evolved than a mouse is incorrect.

The statement implies that there is a goal to evolution and that the monkey represents greater progress to that goal than the mouse. Both species are likely to be well adapted to

their particular environments, which is the outcome of natural selection.

Glossary

adaptation
: heritable trait or behavior in an organism that aids in its survival and reproduction in its present environment

convergent evolution
: process by which groups of organisms independently evolve to similar forms

divergent evolution
: process by which groups of organisms evolve in diverse directions from a common point

homologous structures
: parallel structures in diverse organisms that have a common ancestor

natural selection
: reproduction of individuals with favorable genetic traits that survive environmental change because of those traits, leading to evolutionary change

variation
: genetic differences among individuals in a population

vestigial structure

physical structure present in an organism but that has no apparent function and appears to be from a functional structure in a distant ancestor

Formation of New Species

By the end of this section, you will be able to:

- Define species and describe how species are identified as different
- Describe genetic variables that lead to speciation
- Identify prezygotic and postzygotic reproductive barriers
- Explain allopatric and sympatric speciation
- Describe adaptive radiation

Although all life on earth shares various genetic similarities, only certain organisms combine genetic information by sexual reproduction and have offspring that can then successfully reproduce. Scientists call such organisms members of the same biological species.

The (a) poodle and (b) cocker spaniel can reproduce to produce a breed known as (c) the cockapoo. (credit a: modification of work by Sally Eller, Tom Reese; credit b: modification of work by Jeremy McWilliams; credit c: modification of work by Kathleen Conklin)The (a) African fish eagle is similar in appearance to the (b) bald eagle, but the two birds are members of different species. (credit a: modification of work by Nigel Wedge; credit b: modification of work by U.S. Fish and Wildlife Service)

Species and the Ability to Reproduce

A **species** is a group of individual organisms that interbreed and produce fertile, viable offspring. According to this definition, one species is distinguished from another when, in nature, it is not possible for matings between individuals from each species to produce fertile offspring.

Members of the same species share both external and internal characteristics, which develop from their DNA. The closer relationship two organisms share, the more DNA they have in common, just like people and their families. People’s DNA is likely to be more like their father or mother’s DNA than their cousin or grandparent’s DNA. Organisms of the same species have the highest level of DNA alignment and therefore share characteristics and behaviors that lead to successful reproduction.

Species’ appearance can be misleading in suggesting an ability or inability to mate. For example, even though domestic dogs (*Canis lupus familiaris*) display phenotypic differences, such as size, build, and coat, most dogs can interbreed and produce viable puppies that can mature and sexually reproduce ([link]).

(a) (b) (c)

In other cases, individuals may appear similar although they are not members of the same species. For example, even though bald eagles (*Haliaeetus leucocephalus*) and African fish eagles (*Haliaeetus vocifer*) are both birds and eagles, each belongs to a separate species group ([link]). If humans were to artificially intervene and fertilize the egg of a bald eagle with the sperm of an African fish eagle and a chick did hatch, that offspring, called a **hybrid** (a cross between two species), would probably be infertile—unable to successfully reproduce after it reached maturity. Different species may have different genes that are active in development; therefore, it may not be possible to develop a viable offspring with two different sets of directions. Thus, even though hybridization may take place, the two species still remain separate.

(a) (b)

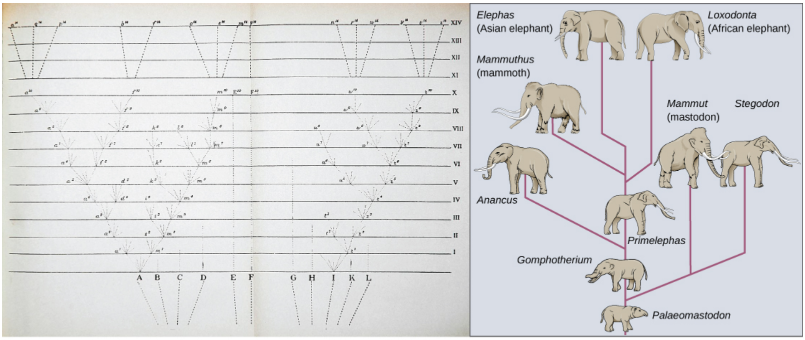
Populations of species share a gene pool: a collection of all the variants of genes in the species. Again, the basis to any changes in a group or population of organisms must be genetic for this is the only way to share and pass on traits. When variations occur within a species, they can only be passed to the next generation along two main pathways: asexual reproduction or sexual reproduction. The change will be passed on asexually simply if the reproducing cell possesses the changed trait. For the changed trait to be passed on by sexual reproduction, a gamete, such as a sperm or egg cell, must possess the changed trait. In other words, sexually-reproducing organisms can experience several genetic changes in their body cells, but if these changes do not occur in a sperm or egg cell, the changed trait will never reach the next generation. Only heritable traits can evolve. Therefore, reproduction plays a paramount role for genetic change to take root in a population or species. In short, organisms must be able to reproduce with each other to pass new traits to offspring.

The only illustration in Darwin's *On the Origin of Species* is (a) a diagram showing speciation events leading to biological diversity. The diagram shows similarities to phylogenetic charts that are drawn today to illustrate the relationships of species. (b) Modern elephants evolved from the *Palaeomastodon*, a species that lived in Egypt 35–50 million years ago.

Speciation

The biological definition of species, which works for sexually reproducing organisms, is a group of actually or potentially interbreeding individuals. There are exceptions to this rule. Many species are similar enough that hybrid offspring are possible and may often occur in nature, but for the majority of species this rule generally holds. In fact, the presence in nature of hybrids between similar species suggests that they may have descended from a single interbreeding species, and the speciation process may not yet be completed.

Given the extraordinary diversity of life on the planet there must be mechanisms for **speciation**: the formation of two species from one original species. Darwin envisioned this process as a branching event and diagrammed the process in the only illustration found in *On the Origin of Species* ([link]**a**). Compare this illustration to the diagram of elephant evolution ([link]**b**), which shows that as one species changes over time, it branches to form more than one new species, repeatedly, as long as the population survives or until the organism becomes extinct.



(a) (b)

For speciation to occur, two new populations must be formed from one original population and they must evolve in such a way that it becomes impossible for individuals from the two new populations to interbreed. Biologists have proposed mechanisms by which this could occur that fall into two broad categories. **Allopatric speciation** (allo- = "other"; -patric = "homeland") involves geographic separation of populations from a parent species and subsequent evolution. **Sympatric speciation** (sym- = "same"; -patric = "homeland") involves speciation occurring within a parent species remaining in one location.

Biologists think of speciation events as the splitting of one ancestral species into two descendant species. There is no reason why there might not be more than two species formed at one time except that it is less likely and multiple events can be conceptualized as single splits occurring close in time.

The northern spotted owl and the Mexican spotted

owl inhabit geographically separate locations with different climates and ecosystems. The owl is an example of allopatric speciation. (credit "northern spotted owl": modification of work by John and Karen Hollingsworth; credit "Mexican spotted owl": modification of work by Bill Radke) The honeycreeper birds illustrate adaptive radiation. From one original species of bird, multiple others evolved, each with its own distinctive characteristics.

Allopatric Speciation

A geographically continuous population has a gene pool that is relatively homogeneous. Gene flow, the movement of alleles across the range of the species, is relatively free because individuals can move and then mate with individuals in their new location. Thus, the frequency of an allele at one end of a distribution will be similar to the frequency of the allele at the other end. When populations become geographically discontinuous, that free-flow of alleles is prevented. When that separation lasts for a period of time, the two populations are able to evolve along different trajectories. Thus, their allele frequencies at numerous genetic loci gradually become more and more different as new alleles independently arise by mutation in each population. Typically, environmental conditions, such as climate, resources, predators, and competitors for the two populations will differ causing natural

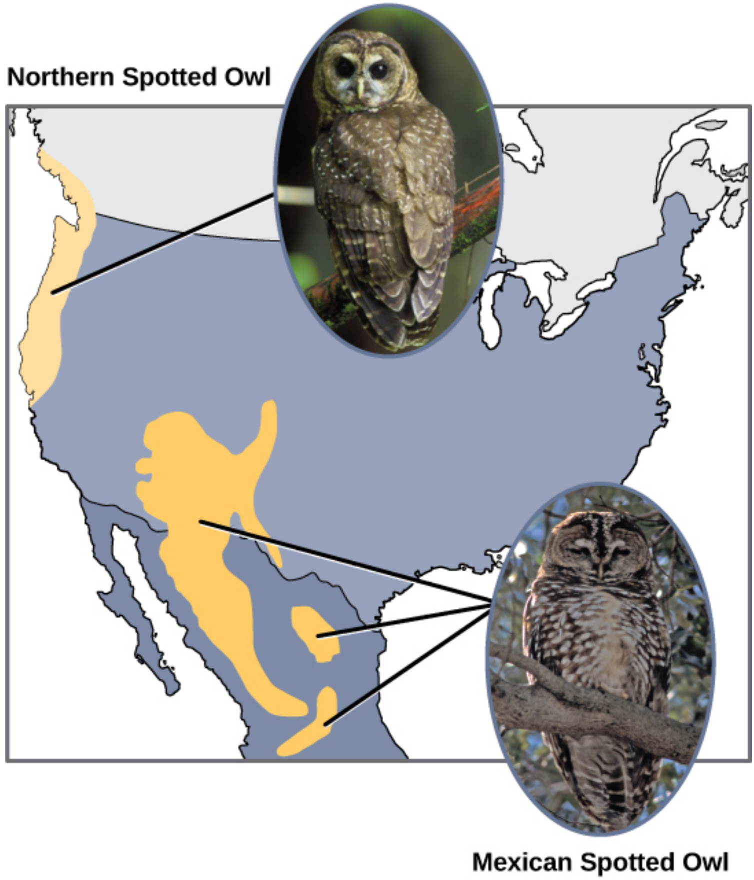
selection to favor divergent adaptations in each group.

Isolation of populations leading to allopatric speciation can occur in a variety of ways: a river forming a new branch, erosion forming a new valley, a group of organisms traveling to a new location without the ability to return, or seeds floating over the ocean to an island. The nature of the geographic separation necessary to isolate populations depends entirely on the biology of the organism and its potential for dispersal. If two flying insect populations took up residence in separate nearby valleys, chances are, individuals from each population would fly back and forth continuing gene flow. However, if two rodent populations became divided by the formation of a new lake, continued gene flow would be unlikely; therefore, speciation would be more likely.

Biologists group allopatric processes into two categories: dispersal and vicariance. **Dispersal** is when a few members of a species move to a new geographical area, and **vicariance** is when a natural situation arises to physically divide organisms.

Scientists have documented numerous cases of allopatric speciation taking place. For example, along the west coast of the United States, two separate sub-species of spotted owls exist. The northern spotted owl has genetic and phenotypic

differences from its close relative: the Mexican spotted owl, which lives in the south ([link]).

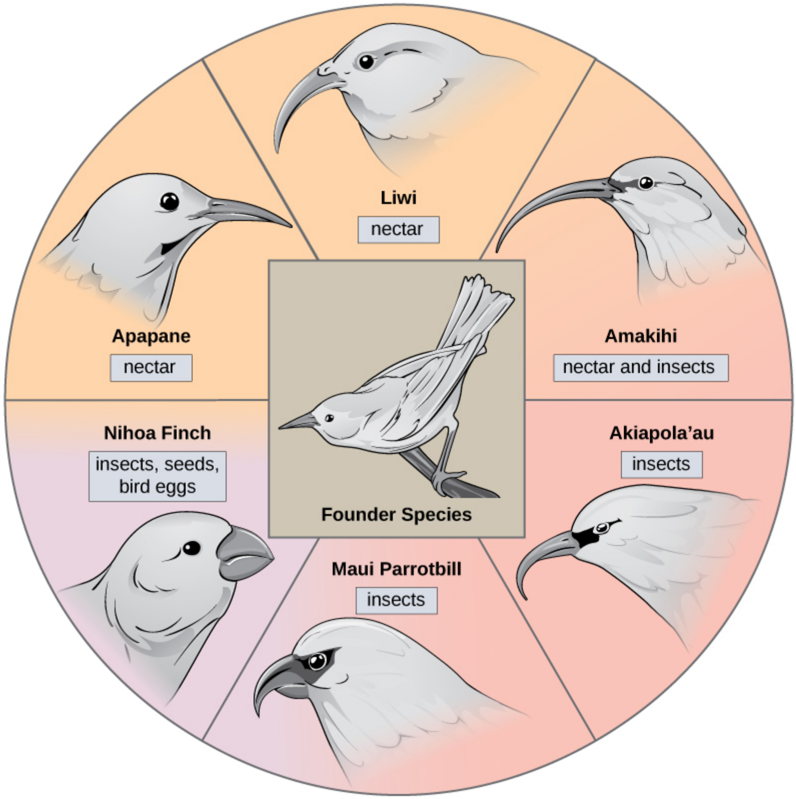


Additionally, scientists have found that the further the distance between two groups that once were the same species, the more likely it is that speciation will occur. This seems logical because as the distance increases, the various environmental factors would likely have less in common than locations in close proximity. Consider the two owls: in the north, the climate is cooler than in the south; the types of organisms in each ecosystem differ, as

do their behaviors and habits; also, the hunting habits and prey choices of the southern owls vary from the northern owls. These variances can lead to evolved differences in the owls, and speciation likely will occur.

Adaptive Radiation

In some cases, a population of one species disperses throughout an area, and each finds a distinct niche or isolated habitat. Over time, the varied demands of their new lifestyles lead to multiple speciation events originating from a single species. This is called **adaptive radiation** because many adaptations evolve from a single point of origin; thus, causing the species to radiate into several new ones. Island archipelagos like the Hawaiian Islands provide an ideal context for adaptive radiation events because water surrounds each island which leads to geographical isolation for many organisms. The Hawaiian honeycreeper illustrates one example of adaptive radiation. From a single species, called the founder species, numerous species have evolved, including the six shown in [link].



Notice the differences in the species' beaks in [link]. Evolution in response to natural selection based on specific food sources in each new habitat led to evolution of a different beak suited to the specific food source. The seed-eating bird has a thicker, stronger beak which is suited to break hard nuts. The nectar-eating birds have long beaks to dip into flowers to reach the nectar. The insect-eating birds have beaks like swords, appropriate for stabbing and impaling insects. Darwin's finches are another example of adaptive radiation in an archipelago.

Link to Learning

Click through this interactive site to see how island birds evolved in evolutionary increments from 5 million years ago to today.

Autopolyploidy results when mitosis is not followed by cytokinesis. Alloploidy results when two species mate to produce viable offspring. In the example shown, a normal gamete from one species fuses with a polyploidy gamete from another. Two matings are necessary to produce viable offspring.

Sympatric Speciation

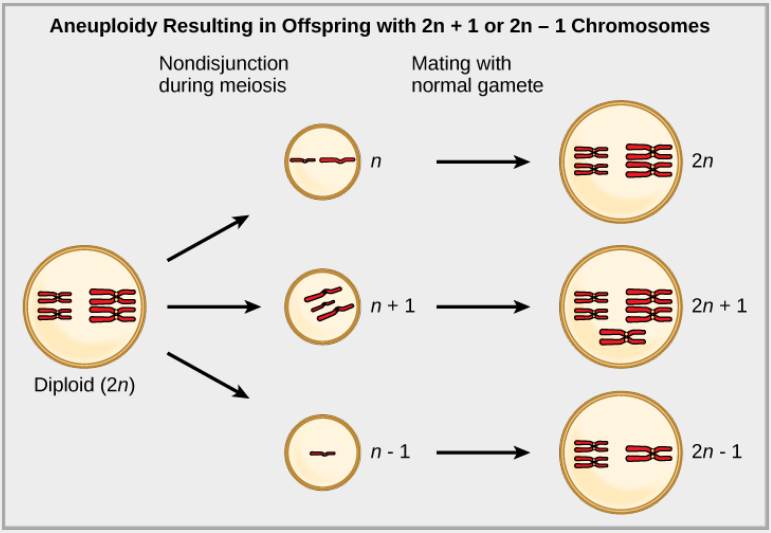
Can divergence occur if no physical barriers are in place to separate individuals who continue to live and reproduce in the same habitat? The answer is yes. The process of speciation within the same space is called sympatric speciation; the prefix “sym” means same, so “sympatric” means “same homeland” in contrast to “allopatric” meaning

“other homeland.” A number of mechanisms for sympatric speciation have been proposed and studied.

One form of sympatric speciation can begin with a serious chromosomal error during cell division. In a normal cell division event chromosomes replicate, pair up, and then separate so that each new cell has the same number of chromosomes. However, sometimes the pairs separate and the end cell product has too many or too few individual chromosomes in a condition called **aneuploidy** ([link]).

Art Connection

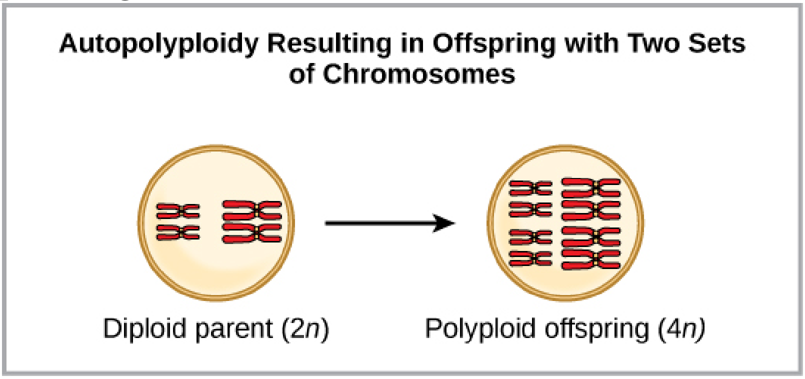
Aneuploidy results when the gametes have too many or too few chromosomes due to nondisjunction during meiosis. In the example shown here, the resulting offspring will have $2n+1$ or $2n$-1 chromosomes



Which is most likely to survive, offspring with $2n+1$ chromosomes or offspring with $2n$-1 chromosomes?

Polyploidy is a condition in which a cell or organism has an extra set, or sets, of chromosomes. Scientists have identified two main types of polyploidy that can lead to reproductive isolation of an individual in the polyploidy state. Reproductive isolation is the inability to interbreed. In some cases, a polyploid individual will have two or more complete sets of chromosomes from its own species in a condition called **autopolyploidy** ([link]). The prefix “auto-” means “self,” so the term means multiple chromosomes from one’s own species. Polyploidy results from an error in meiosis in which all of the chromosomes move into one cell instead of

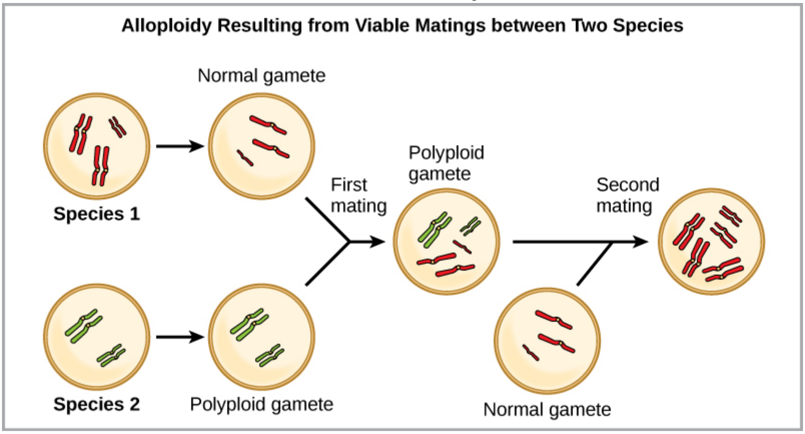
separating.



For example, if a plant species with $2n = 6$ produces autopolyploid gametes that are also diploid ($2n = 6$, when they should be $n = 3$), the gametes now have twice as many chromosomes as they should have. These new gametes will be incompatible with the normal gametes produced by this plant species. However, they could either self-pollinate or reproduce with other autopolyploid plants with gametes having the same diploid number. In this way, sympatric speciation can occur quickly by forming offspring with $4n$ called a tetraploid. These individuals would immediately be able to reproduce only with those of this new kind and not those of the ancestral species.

The other form of polyploidy occurs when individuals of two different species reproduce to form a viable offspring called an **allopolyploid**. The prefix “allo-” means “other” (recall from allopatric): therefore, an allopolyploid occurs when gametes from two different species combine. [link] illustrates

one possible way an allopolyploid can form. Notice how it takes two generations, or two reproductive acts, before the viable fertile hybrid results.



The cultivated forms of wheat, cotton, and tobacco plants are all allopolyploids. Although polyploidy occurs occasionally in animals, it takes place most commonly in plants. (Animals with any of the types of chromosomal aberrations described here are unlikely to survive and produce normal offspring.) Scientists have discovered more than half of all plant species studied relate back to a species evolved through polyploidy. With such a high rate of polyploidy in plants, some scientists hypothesize that this mechanism takes place more as an adaptation than as an error.

These two related frog species exhibit temporal reproductive isolation. (a) *Rana aurora* breeds earlier in the year than (b) *Rana boylii*. (credit a: modification of work by Mark R. Jennings, USFWS; credit b: modification of work by Alessandro Catenazzi)Speciation can occur when two

populations occupy different habitats. The habitats need not be far apart. The cricket (a) *Gryllus pennsylvanicus* prefers sandy soil, and the cricket (b) *Gryllus firmus* prefers loamy soil. The two species can live in close proximity, but because of their different soil preferences, they became genetically isolated. The shape of the male reproductive organ varies among male damselfly species, and is only compatible with the female of that species. Reproductive organ incompatibility keeps the species reproductively isolated. Some flowers have evolved to attract certain pollinators. The (a) wide foxglove flower is adapted for pollination by bees, while the (b) long, tube-shaped trumpet creeper flower is adapted for pollination by humming birds. Cichlid fish from Lake Apoyeque, Nicaragua, show evidence of sympatric speciation. Lake Apoyeque, a crater lake, is 1800 years old, but genetic evidence indicates that the lake was populated only 100 years ago by a single population of cichlid fish. Nevertheless, two populations with distinct morphologies and diets now exist in the lake, and scientists believe these populations may be in an early stage of speciation.

Reproductive Isolation

Given enough time, the genetic and phenotypic divergence between populations will affect characters that influence reproduction: if individuals of the two populations were to be brought together,

mating would be less likely, but if mating occurred, offspring would be non-viable or infertile. Many types of diverging characters may affect the **reproductive isolation**, the ability to interbreed, of the two populations.

Reproductive isolation can take place in a variety of ways. Scientists organize them into two groups: prezygotic barriers and postzygotic barriers. Recall that a zygote is a fertilized egg: the first cell of the development of an organism that reproduces sexually. Therefore, a **prezygotic barrier** is a mechanism that blocks reproduction from taking place; this includes barriers that prevent fertilization when organisms attempt reproduction. A **postzygotic barrier** occurs after zygote formation; this includes organisms that don’t survive the embryonic stage and those that are born sterile.

Some types of prezygotic barriers prevent reproduction entirely. Many organisms only reproduce at certain times of the year, often just annually. Differences in breeding schedules, called **temporal isolation**, can act as a form of reproductive isolation. For example, two species of frogs inhabit the same area, but one reproduces from January to March, whereas the other reproduces from March to May ([link]).

(a) (b)

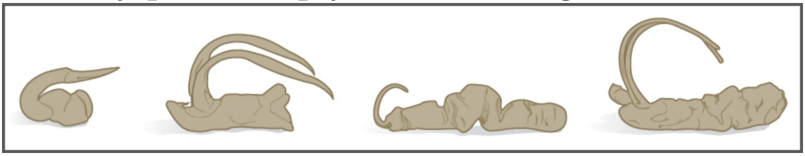
In some cases, populations of a species move or are moved to a new habitat and take up residence in a place that no longer overlaps with the other populations of the same species. This situation is called **habitat isolation**. Reproduction with the parent species ceases, and a new group exists that is now reproductively and genetically independent. For example, a cricket population that was divided after a flood could no longer interact with each other. Over time, the forces of natural selection, mutation, and genetic drift will likely result in the divergence of the two groups ([link]).

(a) *Gryllus pennsylvanicus* prefers sandy soil. (b) *Gryllus firmus* prefers loamy soil.

Behavioral isolation occurs when the presence or absence of a specific behavior prevents reproduction

from taking place. For example, male fireflies use specific light patterns to attract females. Various species of fireflies display their lights differently. If a male of one species tried to attract the female of another, she would not recognize the light pattern and would not mate with the male.

Other prezygotic barriers work when differences in their gamete cells (eggs and sperm) prevent fertilization from taking place; this is called a **gametic barrier**. Similarly, in some cases closely related organisms try to mate, but their reproductive structures simply do not fit together. For example, damselfly males of different species have differently shaped reproductive organs. If one species tries to mate with the female of another, their body parts simply do not fit together. ([link]).



In plants, certain structures aimed to attract one type of pollinator simultaneously prevent a different pollinator from accessing the pollen. The tunnel through which an animal must access nectar can vary widely in length and diameter, which prevents the plant from being cross-pollinated with a different species ([link]).

(a) Honeybee drinking nectar from a foxglove flower

(b) Ruby-throated hummingbird drinking nectar from a trumpet creeper flower

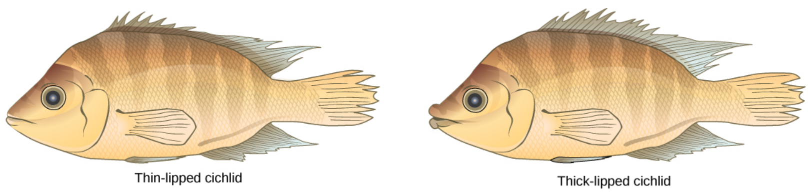
When fertilization takes place and a zygote forms, postzygotic barriers can prevent reproduction. Hybrid individuals in many cases cannot form normally in the womb and simply do not survive past the embryonic stages. This is called **hybrid inviability** because the hybrid organisms simply are not viable. In another postzygotic situation, reproduction leads to the birth and growth of a hybrid that is sterile and unable to reproduce offspring of their own; this is called hybrid sterility.

Habitat Influence on Speciation

Sympatric speciation may also take place in ways other than polyploidy. For example, consider a species of fish that lives in a lake. As the population grows, competition for food also grows. Under pressure to find food, suppose that a group of these fish had the genetic flexibility to discover and feed off another resource that was unused by the other fish. What if this new food source was found at a different depth of the lake? Over time, those feeding on the second food source would interact more with

each other than the other fish; therefore, they would breed together as well. Offspring of these fish would likely behave as their parents: feeding and living in the same area and keeping separate from the original population. If this group of fish continued to remain separate from the first population, eventually sympatric speciation might occur as more genetic differences accumulated between them.

This scenario does play out in nature, as do others that lead to reproductive isolation. One such place is Lake Victoria in Africa, famous for its sympatric speciation of cichlid fish. Researchers have found hundreds of sympatric speciation events in these fish, which have not only happened in great number, but also over a short period of time. [link] shows this type of speciation among a cichlid fish population in Nicaragua. In this locale, two types of cichlids live in the same geographic location but have come to have different morphologies that allow them to eat various food sources.



Section Summary

Speciation occurs along two main pathways: geographic separation (allopatric speciation) and

through mechanisms that occur within a shared habitat (sympatric speciation). Both pathways isolate a population reproductively in some form. Mechanisms of reproductive isolation act as barriers between closely related species, enabling them to diverge and exist as genetically independent species. Prezygotic barriers block reproduction prior to formation of a zygote, whereas postzygotic barriers block reproduction after fertilization occurs. For a new species to develop, something must cause a breach in the reproductive barriers. Sympatric speciation can occur through errors in meiosis that form gametes with extra chromosomes (polyploidy). Autopolyploidy occurs within a single species, whereas allopolyploidy occurs between closely related species.

Art Connections

[link] Which is most likely to survive, offspring with $2n+1$ chromosomes or offspring with $2n$-1 chromosomes?

[link] Loss of genetic material is almost always lethal, so offspring with $2n+1$ chromosomes are more likely to survive.

Review Questions

Which situation would most likely lead to allopatric speciation?

1. flood causes the formation of a new lake.
2. A storm causes several large trees to fall down.
3. A mutation causes a new trait to develop.
4. An injury causes an organism to seek out a new food source.

A

What is the main difference between dispersal and vicariance?

1. One leads to allopatric speciation, whereas the other leads to sympatric speciation.
2. One involves the movement of the organism, and the other involves a change in the environment.
3. One depends on a genetic mutation occurring, and the other does not.
4. One involves closely related organisms, and the other involves only individuals of the same species.

B

Which variable increases the likelihood of allopatric speciation taking place more quickly?

1. lower rate of mutation
2. longer distance between divided groups
3. increased instances of hybrid formation
4. equivalent numbers of individuals in each population

B

What is the main difference between autopolyploid and allopolyploid?

1. the number of chromosomes
2. the functionality of the chromosomes
3. the source of the extra chromosomes
4. the number of mutations in the extra chromosomes

C

Which reproductive combination produces hybrids?

1. when individuals of the same species in different geographical areas reproduce
2. when any two individuals sharing the same habitat reproduce
3. when members of closely related species reproduce
4. when offspring of the same parents reproduce

C

Which condition is the basis for a species to be reproductively isolated from other members?

1. It does not share its habitat with related species.
2. It does not exist out of a single habitat.
3. It does not exchange genetic information with other species.
4. It does not undergo evolutionary changes for a significant period of time.

C

Which situation is *not* an example of a prezygotic barrier?

1. Two species of turtles breed at different

times of the year.
2. Two species of flowers attract different pollinators.
3. Two species of birds display different mating dances.
4. Two species of insects produce infertile offspring.

D

Free Response

Why do island chains provide ideal conditions for adaptive radiation to occur?

Organisms of one species can arrive to an island together and then disperse throughout the chain, each settling into different niches and exploiting different food resources to reduce competition.

Two species of fish had recently undergone sympatric speciation. The males of each species had a different coloring through which the females could identify and choose a partner

from her own species. After some time, pollution made the lake so cloudy that it was hard for females to distinguish colors. What might take place in this situation?

It is likely the two species would start to reproduce with each other. Depending on the viability of their offspring, they may fuse back into one species.

Why can polyploidy individuals lead to speciation fairly quickly?

The formation of gametes with new *n* numbers can occur in one generation. After a couple of generations, enough of these new hybrids can form to reproduce together as a new species.

Glossary

adaptive radiation
: speciation when one species radiates out to form several other species

allopatric speciation
: speciation that occurs via geographic separation

allopolyploid
: polyploidy formed between two related, but separate species

aneuploidy
: condition of a cell having an extra chromosome or missing a chromosome for its species

autopolyploid
: polyploidy formed within a single species

behavioral isolation
: type of reproductive isolation that occurs when a specific behavior or lack of one prevents reproduction from taking place

dispersal
: allopatric speciation that occurs when a few members of a species move to a new geographical area

gametic barrier
: prezygotic barrier occurring when closely related individuals of different species mate, but differences in their gamete cells (eggs and sperm) prevent fertilization from taking place

habitat isolation
: reproductive isolation resulting when populations of a species move or are moved to a new habitat, taking up residence in a

place that no longer overlaps with the other populations of the same species

hybrid
: offspring of two closely related individuals, not of the same species

postzygotic barrier
: reproductive isolation mechanism that occurs after zygote formation

prezygotic barrier
: reproductive isolation mechanism that occurs before zygote formation

reproductive isolation
: situation that occurs when a species is reproductively independent from other species; this may be brought about by behavior, location, or reproductive barriers

speciation
: formation of a new species

species
: group of populations that interbreed and produce fertile offspring

sympatric speciation
: speciation that occurs in the same geographic space

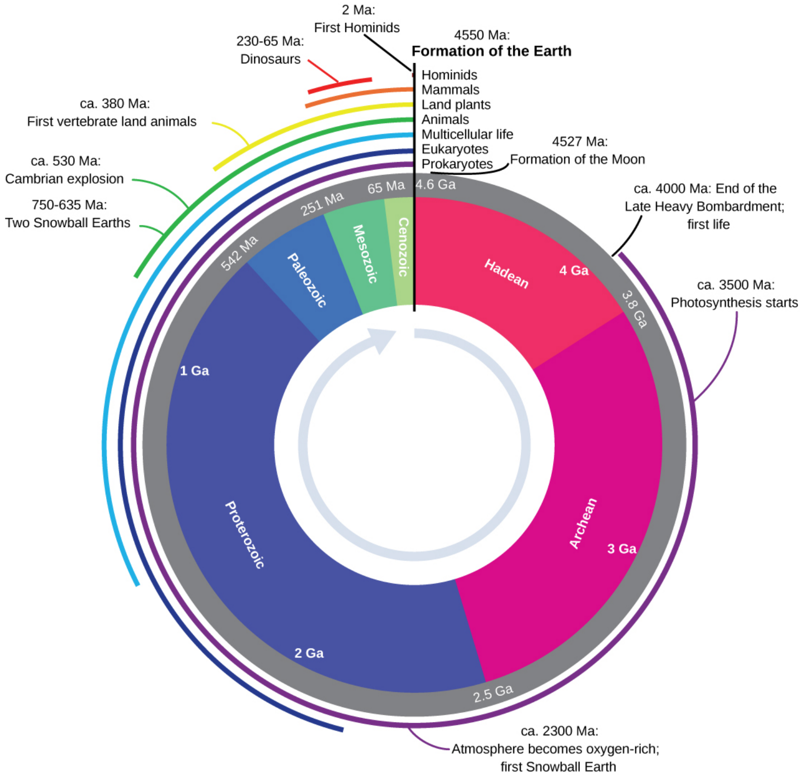
temporal isolation

differences in breeding schedules that can act as a form of prezygotic barrier leading to reproductive isolation

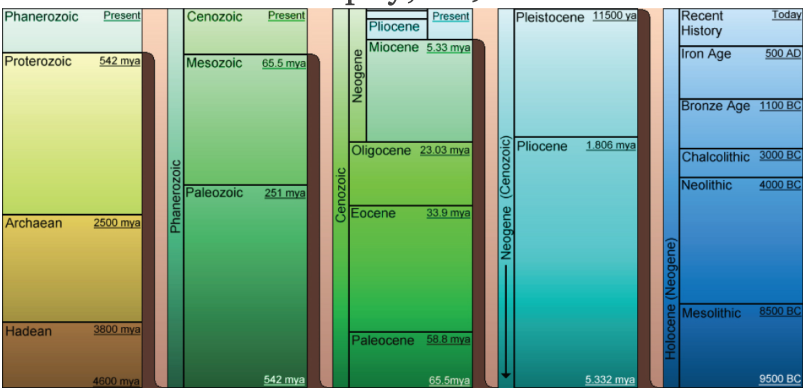
vicariance
: allopatric speciation that occurs when something in the environment separates organisms of the same species into separate groups

Geological Time

Geological Time Clock



Geological Time Chart
(credit: Richard S. Murphy, Jr.)



Population Evolution

By the end of this section, you will be able to do the following:

- Define population genetics and describe how scientists use population genetics in studying population evolution
- Define the Hardy-Weinberg principle and discuss its importance

People did not understand the mechanisms of inheritance, or genetics, at the time Charles Darwin and Alfred Russel Wallace were developing their idea of natural selection. This lack of knowledge was a stumbling block to understanding many aspects of evolution. The predominant (and incorrect) genetic theory of the time, blending inheritance, made it difficult to understand how natural selection might operate. Darwin and Wallace were unaware of the Austrian monk Gregor Mendel's 1866 publication "Experiments in Plant Hybridization", which came out not long after Darwin's book, *On the Origin of Species*. Scholars rediscovered Mendel's work in the early twentieth century at which time geneticists were rapidly coming to an understanding of the basics of inheritance. Initially, the newly discovered particulate nature of genes made it difficult for biologists to understand how gradual evolution could occur. However, over the next few decades scientists integrated genetics and evolution in what

became known as the **modern synthesis—**the coherent understanding of the relationship between natural selection and genetics that took shape by the 1940s. Generally, this concept is generally accepted today. In short, the modern synthesis describes how evolutionary processes, such as natural selection, can affect a population's genetic makeup, and, in turn, how this can result in the gradual evolution of populations and species. The theory also connects population change over time **(microevolution)**, with the processes that gave rise to new species and higher taxonomic groups with widely divergent characters, called **(macroevolution)**.

Everyday Connection

Evolution and Flu Vaccines

Every fall, the media starts reporting on flu vaccinations and potential outbreaks. Scientists, health experts, and institutions determine recommendations for different parts of the population, predict optimal production and inoculation schedules, create vaccines, and set up clinics to provide inoculations. You may think of the annual flu shot as media hype, an important health protection, or just a briefly uncomfortable prick in your arm. However, do you think of it in terms of evolution?

The media hype of annual flu shots is scientifically grounded in our understanding of evolution. Each

year, scientists across the globe strive to predict the flu strains that they anticipate as most widespread and harmful in the coming year. They base this knowledge on how flu strains have evolved over time and over the past few flu seasons. Scientists then work to create the most effective vaccine to combat those selected strains. Pharmaceutical companies produce hundreds of millions of doses in a short period in order to provide vaccinations to key populations at the optimal time.
Because viruses, like the flu, evolve very quickly (especially in evolutionary time), this poses quite a challenge. Viruses mutate and replicate at a fast rate, so the vaccine developed to protect against last year's flu strain may not provide the protection one needs against the coming year's strain. Evolution of these viruses means continued adaptions to ensure survival, including adaptations to survive previous vaccines.

Sahar S. Hanania, Dhia S. Hassawi, and Nidal M. Irshaid, "Allele Frequency and Molecular Genotypes of ABO Blood Group System in a Jordanian Population," *Journal of Medical Sciences* 7 (2007): 51-58, doi:10.3923/jms.2007.51.58.

Population Genetics

Recall that a gene for a particular character may

have several alleles, or variants, that code for different traits associated with that character. For example, in the ABO blood type system in humans, three alleles determine the particular blood-type carbohydrate on the surface of red blood cells. Each individual in a population of diploid organisms can only carry two alleles for a particular gene, but more than two may be present in the individuals that comprise the population. Mendel followed alleles as they were inherited from parent to offspring. In the early twentieth century, biologists in the area of **population genetics** began to study how selective forces change a population through changes in allele and genotypic frequencies.

The **allele frequency** (or gene frequency) is the rate at which a specific allele appears within a population. Until now we have discussed evolution as a change in the characteristics of a population of organisms, but behind that phenotypic change is genetic change. In population genetics, scientists define the term evolution as a change in the allele's frequency in a population. Using the ABO blood type system as an example, the frequency of one of the alleles, I^A, is the number of copies of that allele divided by all the copies of the ABO gene in the population. For example, a study in Jordan[footnote] found a frequency of I^A to be 26.1 percent. The I^B and I^0 alleles comprise 13.4 percent and 60.5 percent of the alleles respectively, and all of the frequencies added up to 100 percent. A change in

this frequency over time would constitute evolution in the population.

The allele frequency within a given population can change depending on environmental factors; therefore, certain alleles become more widespread than others during the natural selection process. Natural selection can alter the population’s genetic makeup. An example is if a given allele confers a phenotype that allows an individual to better survive or have more offspring. Because many of those offspring will also carry the beneficial allele, and often the corresponding phenotype, they will have more offspring of their own that also carry the allele, thus, perpetuating the cycle. Over time, the allele will spread throughout the population. Some alleles will quickly become fixed in this way, meaning that every individual of the population will carry the allele, while detrimental mutations may be swiftly eliminated if derived from a dominant allele from the gene pool. The **gene pool** is the sum of all the alleles in a population.

Sometimes, allele frequencies within a population change randomly with no advantage to the population over existing allele frequencies. We call this phenomenon genetic drift. Natural selection and genetic drift usually occur simultaneously in populations and are not isolated events. It is hard to determine which process dominates because it is often nearly impossible to determine the cause of

change in allele frequencies at each occurrence. We call an event that initiates an allele frequency change in an isolated part of the population, which is not typical of the original population, the **founder effect**. Natural selection, random drift, and founder effects can lead to significant changes in a population's genome.

Hardy-Weinberg Principle of Equilibrium

In the early twentieth century, English mathematician Godfrey Hardy and German physician Wilhelm Weinberg stated the principle of equilibrium to describe the population's genetic makeup. The theory, which later became known as the Hardy-Weinberg principle of equilibrium, states that a population’s allele and genotype frequencies are inherently stable— unless some kind of evolutionary force is acting upon the population, neither the allele nor the genotypic frequencies would change. The Hardy-Weinberg principle assumes conditions with no mutations, migration, emigration, or selective pressure for or against genotype, plus an infinite population. While no population can satisfy those conditions, the principle offers a useful model against which to compare real population changes.

Working under this theory, population geneticists represent different alleles as different variables in

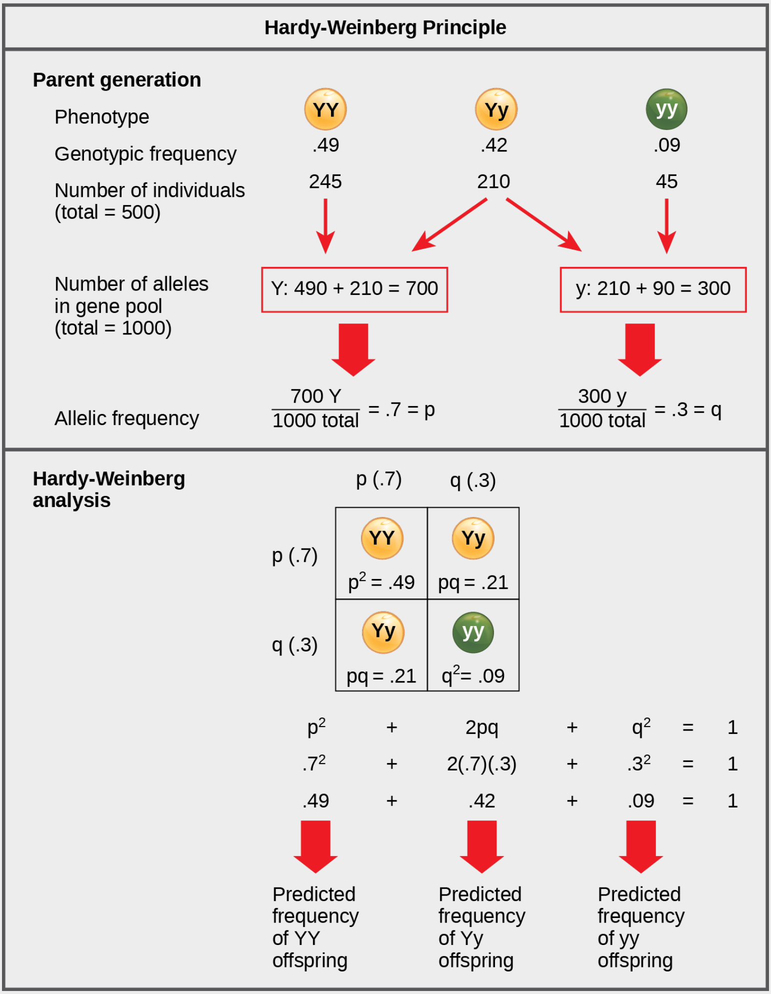
their mathematical models. The variable p, for example, often represents the frequency of a particular allele, say Y for the trait of yellow in Mendel’s peas, while the variable q represents the frequency of y alleles that confer the color green. If these are the only two possible alleles for a given locus in the population, $p + q = 1$. In other words, all the p alleles and all the q alleles comprise all of the alleles for that locus in the population.

However, what ultimately interests most biologists is not the frequencies of different alleles, but the frequencies of the resulting genotypes, known as the population’s **genetic structure**, from which scientists can surmise phenotype distribution. If we observe the phenotype, we can know only the homozygous recessive allele's genotype. The calculations provide an estimate of the remaining genotypes. Since each individual carries two alleles per gene, if we know the allele frequencies (p and q), predicting the genotypes' frequencies is a simple mathematical calculation to determine the probability of obtaining these genotypes if we draw two alleles at random from the gene pool. In the above scenario, an individual pea plant could be pp (YY), and thus produce yellow peas; pq (Yy), also yellow; or qq (yy), and thus produce green peas ([link]). In other words, the frequency of pp individuals is simply p^2; the frequency of pq individuals is 2pq; and the frequency of qq individuals is q^2. Again, if p and q are the only two

possible alleles for a given trait in the population, these genotypes frequencies will sum to one: $p^2 + 2pq + q^2 = 1$.

Visual Connection

When populations are in the Hardy-Weinberg equilibrium, the allelic frequency is stable from generation to generation and we can determine the allele distribution from the Hardy-Weinberg equation. If the allelic frequency measured in the field differs from the predicted value, scientists can make inferences about what evolutionary forces are at play.



In plants, violet flower color (V) is dominant over white (v). If $p = 0.8$ and $q = 0.2$ in a population of 500 plants, how many individuals would you expect to be homozygous dominant (VV), heterozygous (Vv), and homozygous recessive (vv)? How many plants would you expect to have violet flowers, and how many would have white flowers?

In theory, if a population is at equilibrium—that is, there are no evolutionary forces acting upon it—generation after generation would have the same gene pool and genetic structure, and these equations would all hold true all of the time. Of course, even Hardy and Weinberg recognized that no natural population is immune to evolution. Populations in nature are constantly changing in genetic makeup due to drift, mutation, possibly migration, and selection. As a result, the only way to determine the exact distribution of phenotypes in a population is to go out and count them. However, the Hardy-Weinberg principle gives scientists a mathematical baseline of a non-evolving population to which they can compare evolving populations and thereby infer what evolutionary forces might be at play. If the frequencies of alleles or genotypes deviate from the value expected from the Hardy-Weinberg equation, then the population is evolving.

Link to Learning
Use this online calculator to determine a population's genetic structure.

Section Summary

The modern synthesis of evolutionary theory grew out of the cohesion of Darwin’s, Wallace’s, and Mendel’s thoughts on evolution and heredity, along with the more modern study of population genetics. It describes the evolution of populations and species, from small-scale changes among individuals to large-scale changes over paleontological time periods. To understand how organisms evolve, scientists can track populations’ allele frequencies over time. If they differ from generation to generation, scientists can conclude that the population is not in Hardy-Weinberg equilibrium, and is thus evolving.

Visual Connection Questions

[link] In plants, violet flower color (V) is dominant over white (v). If $p = .8$ and $q = 0.2$ in a population of 500 plants, how many individuals would you expect to be homozygous dominant (VV), heterozygous (Vv), and homozygous recessive (vv)? How many plants would you expect to have violet flowers, and how many would have white flowers?

[link] The expected distribution is 320 VV, 160Vv, and 20 vv plants. Plants with VV or Vv

genotypes would have violet flowers, and plants with the vv genotype would have white flowers, so a total of 480 plants would be expected to have violet flowers, and 20 plants would have white flowers.

Review Questions

What is the difference between micro- and macroevolution?

1. Microevolution describes the evolution of small organisms, such as insects, while macroevolution describes the evolution of large organisms, like people and elephants.
2. Microevolution describes the evolution of microscopic entities, such as molecules and proteins, while macroevolution describes the evolution of whole organisms.
3. Microevolution describes the evolution of organisms in populations, while macroevolution describes the evolution of species over long periods of time.
4. Microevolution describes the evolution of organisms over their lifetimes, while macroevolution describes the evolution of organisms over multiple generations.

C

Population genetics is the study of:

1. how selective forces change the allele frequencies in a population over time
2. the genetic basis of population-wide traits
3. whether traits have a genetic basis
4. the degree of inbreeding in a population

A

Which of the following populations is not in Hardy-Weinberg equilibrium?

1. a population with 12 homozygous recessive individuals (yy), 8 homozygous dominant individuals (YY), and 4 heterozygous individuals (Yy)
2. a population in which the allele frequencies do not change over time
3. $p^2 + 2pq + q^2 = 1$
4. a population undergoing natural selection

D

One of the original Amish colonies rose from a

ship of colonists that came from Europe. The ship's captain, who had polydactyly, a rare dominant trait, was one of the original colonists. Today, we see a much higher frequency of polydactyly in the Amish population. This is an example of:

1. natural selection
2. genetic drift
3. founder effect
4. b and c

D

Critical Thinking Questions

Solve for the genetic structure of a population with 12 homozygous recessive individuals (yy), 8 homozygous dominant individuals (YY), and 4 heterozygous individuals (Yy).

$p = (8*2 + 4)/48 = .42$; $q = (12*2 + 4)/48 = .58$; $p^2 = .17$; $2pq = .48$; $q^2 = .34$

Explain the Hardy-Weinberg principle of

equilibrium theory.

The Hardy-Weinberg principle of equilibrium is used to describe the genetic makeup of a population. The theory states that a population's allele and genotype frequencies are inherently stable: unless some kind of evolutionary force is acting upon the population, generation after generation of the population would carry the same genes, and individuals would, as a whole, look essentially the same.

Imagine you are trying to test whether a population of flowers is undergoing evolution. You suspect there is selection pressure on the color of the flower: bees seem to cluster around the red flowers more often than the blue flowers. In a separate experiment, you discover blue flower color is dominant to red flower color. In a field, you count 600 blue flowers and 200 red flowers. What would you expect the genetic structure of the flowers to be?

Red is recessive so q2 = 200/800 = 0.25; q = 0.5; p = 1 - q = 0.5; p2 = 0.25; 2pq = 0.5. You would expect 200 homozygous blue flowers, 400 heterozygous blue flowers, and 200 red flowers.

Glossary

allele frequency
: (also, gene frequency) rate at which a specific allele appears within a population

founder effect
: event that initiates an allele frequency change in part of the population, which is not typical of the original population

gene pool
: all the alleles that the individuals in the population carry

genetic structure
: distribution of the different possible genotypes in a population

macroevolution
: broader scale evolutionary changes that scientists see over paleontological time

microevolution
: changes in a population's genetic structure

modern synthesis
: overarching evolutionary paradigm that took shape by the 1940s and scientists generally accept today

population genetics
: study of how selective forces change the allele frequencies in a population over time

Population Genetics

By the end of this section, you will be able to:

- Describe the different types of variation in a population
- Explain why only heritable variation can be acted upon by natural selection
- Describe genetic drift and the bottleneck effect
- Explain how each evolutionary force can influence the allele frequencies of a population

Individuals of a population often display different phenotypes, or express different alleles of a particular gene, referred to as polymorphisms. Populations with two or more variations of particular characteristics are called polymorphic. The distribution of phenotypes among individuals, known as the **population variation**, is influenced by a number of factors, including the population's genetic structure and the environment ([link]). Understanding the sources of a phenotypic variation in a population is important for determining how a population will evolve in response to different evolutionary pressures.

The distribution of phenotypes in this litter of kittens illustrates population variation. (credit: Pieter Lanser)

Genetic Variance

Natural selection and some of the other evolutionary forces can only act on heritable traits, namely an organism's genetic code. Because alleles are passed from parent to offspring, those that confer beneficial traits or behaviors may be selected for, while deleterious alleles may be selected against. Acquired traits, for the most part, are not heritable. For example, if an athlete works out in the gym every day, building up muscle strength, the athlete's offspring will not necessarily grow up to be a body builder. If there is a genetic basis for the ability to run fast, on the other hand, this may be passed to a child.

Link to Learning

Before Darwinian evolution became the prevailing theory of the field, French naturalist Jean-Baptiste Lamarck theorized that acquired traits could, in fact, be inherited; while this hypothesis has largely been unsupported, scientists have recently begun to realize that Lamarck was not completely wrong. Visit this site to learn more.

Heritability is the fraction of phenotype variation that can be attributed to genetic differences, or genetic variance, among individuals in a population. The greater the hereditability of a population’s phenotypic variation, the more susceptible it is to the evolutionary forces that act on heritable variation.

The diversity of alleles and genotypes within a population is called **genetic variance**. When scientists are involved in the breeding of a species, such as with animals in zoos and nature preserves,

they try to increase a population's genetic variance to preserve as much of the phenotypic diversity as they can. This also helps reduce the risks associated with **inbreeding**, the mating of closely related individuals, which can have the undesirable effect of bringing together deleterious recessive mutations that can cause abnormalities and susceptibility to disease. For example, a disease that is caused by a rare, recessive allele might exist in a population, but it will only manifest itself when an individual carries two copies of the allele. Because the allele is rare in a normal, healthy population with unrestricted habitat, the chance that two carriers will mate is low, and even then, only 25 percent of their offspring will inherit the disease allele from both parents. While it is likely to happen at some point, it will not happen frequently enough for natural selection to be able to swiftly eliminate the allele from the population, and as a result, the allele will be maintained at low levels in the gene pool. However, if a family of carriers begins to interbreed with each other, this will dramatically increase the likelihood of two carriers mating and eventually producing diseased offspring, a phenomenon known as **inbreeding depression**.

Changes in allele frequencies that are identified in a population can shed light on how it is evolving. In addition to natural selection, there are other evolutionary forces that could be in play: genetic drift, gene flow, mutation, nonrandom mating, and

environmental variances.

A chance event or catastrophe can reduce the genetic variability within a population.A. J. Tipping et al., “Molecular and Genealogical Evidence for a Founder Effect in Fanconi Anemia Families of the Afrikaner Population of South Africa,” *PNAS* 98, no. 10 (2001): 5734-5739, doi: 10.1073/pnas.091402398.

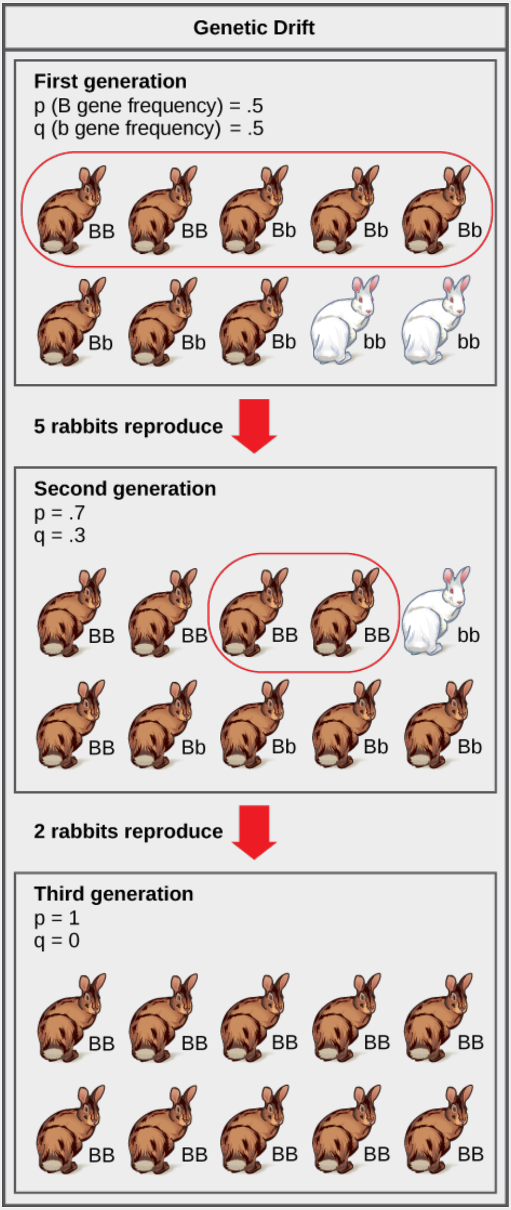
Genetic Drift

The theory of natural selection stems from the observation that some individuals in a population are more likely to survive longer and have more offspring than others; thus, they will pass on more of their genes to the next generation. A big, powerful male gorilla, for example, is much more likely than a smaller, weaker one to become the population’s silverback, the pack’s leader who mates far more than the other males of the group. The pack leader will father more offspring, who share half of his genes, and are likely to also grow bigger and stronger like their father. Over time, the genes for bigger size will increase in frequency in the population, and the population will, as a result, grow larger on average. That is, this would occur if this particular **selection pressure**, or driving selective force, were the only one acting on the population. In other examples, better camouflage or a stronger resistance to drought might pose a selection pressure.

Another way a population's allele and genotype frequencies can change is **genetic drift** ([link]), which is simply the effect of chance. By chance, some individuals will have more offspring than others—not due to an advantage conferred by some genetically-encoded trait, but just because one male happened to be in the right place at the right time (when the receptive female walked by) or because the other one happened to be in the wrong place at the wrong time (when a fox was hunting).

Art Connection

Genetic drift in a population can lead to the elimination of an allele from a population by chance. In this example, rabbits with the brown coat color allele (*B*) are dominant over rabbits with the white coat color allele (*b*). In the first generation, the two alleles occur with equal frequency in the population, resulting in p and q values of .5. Only half of the individuals reproduce, resulting in a second generation with p and q values of .7 and .3, respectively. Only two individuals in the second generation reproduce, and by chance these individuals are homozygous dominant for brown coat color. As a result, in the third generation the recessive *b* allele is lost.



Do you think genetic drift would happen more quickly on an island or on the mainland?

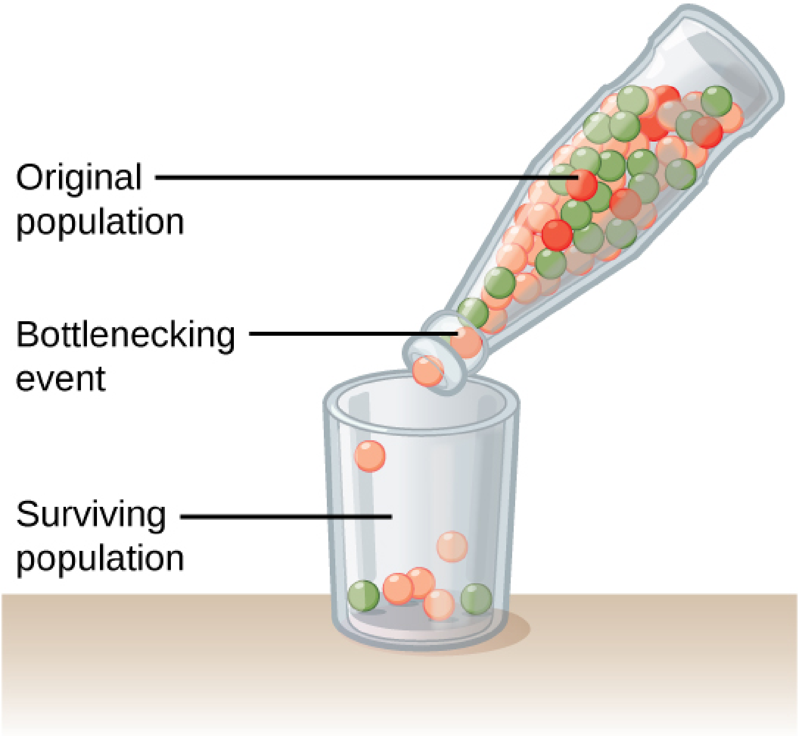
Small populations are more susceptible to the forces of genetic drift. Large populations, on the other hand, are buffered against the effects of chance. If one individual of a population of 10 individuals happens to die at a young age before it leaves any offspring to the next generation, all of its genes—1/10 of the population's gene pool—will be suddenly lost. In a population of 100, that's only 1 percent of the overall gene pool; therefore, it is much less impactful on the population's genetic structure.

Link to Learning

Go to this site to watch an animation of random sampling and genetic drift in action.

Genetic drift can also be magnified by natural events, such as a natural disaster that kills—at random—a large portion of the population. Known

as the **bottleneck effect**, it results in a large portion of the genome suddenly being wiped out ([link]). In one fell swoop, the genetic structure of the survivors becomes the genetic structure of the entire population, which may be very different from the pre-disaster population.



Another scenario in which populations might experience a strong influence of genetic drift is if some portion of the population leaves to start a new population in a new location or if a population gets divided by a physical barrier of some kind. In this situation, those individuals are unlikely to be representative of the entire population, which results in the founder effect. The founder effect

occurs when the genetic structure changes to match that of the new population’s founding fathers and mothers. The founder effect is believed to have been a key factor in the genetic history of the Afrikaner population of Dutch settlers in South Africa, as evidenced by mutations that are common in Afrikaners but rare in most other populations. This is likely due to the fact that a higher-than-normal proportion of the founding colonists carried these mutations. As a result, the population expresses unusually high incidences of Huntington’s disease (HD) and Fanconi anemia (FA), a genetic disorder known to cause blood marrow and congenital abnormalities—even cancer.[footnote]

Link to Learning

Watch this short video to learn more about the founder and bottleneck effects.
https://www.openstaxcollege.org/l/founder_bottle

Scientific Method Connection

Testing the Bottleneck Effect

Question: How do natural disasters affect the genetic structure of a population?

Background: When much of a population is suddenly wiped out by an earthquake or hurricane, the individuals that survive the event are usually a random sampling of the original group. As a result, the genetic makeup of the population can change dramatically. This phenomenon is known as the bottleneck effect.

Hypothesis: Repeated natural disasters will yield different population genetic structures; therefore, each time this experiment is run, the results will vary.

Test the hypothesis: Count out the original population using different colored beads. For example, red, blue, and yellow beads might represent red, blue, and yellow individuals. After recording the number of each individual in the original population, place them all in a bottle with a narrow neck that will only allow a few beads out at a time. Then, pour 1/3 of the bottle's contents into a bowl. This represents the surviving individuals after a natural disaster kills a majority of the population. Count the number of the different colored beads in the bowl, and record it. Then, place all of the beads back in the bottle and repeat the experiment four more times.

Analyze the data: Compare the five populations that resulted from the experiment. Do the

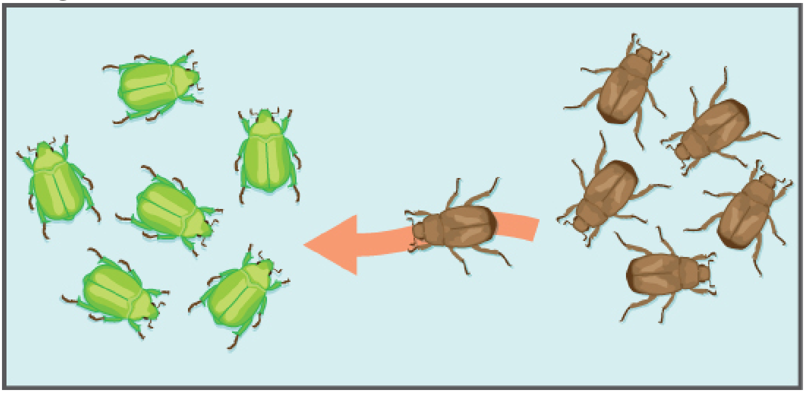
populations all contain the same number of different colored beads, or do they vary? Remember, these populations all came from the same exact parent population.
Form a conclusion: Most likely, the five resulting populations will differ quite dramatically. This is because natural disasters are not selective—they kill and spare individuals at random. Now think about how this might affect a real population. What happens when a hurricane hits the Mississippi Gulf Coast? How do the seabirds that live on the beach fare?

Gene flow can occur when an individual travels from one geographic location to another.

Gene Flow

Another important evolutionary force is **gene flow**: the flow of alleles in and out of a population due to the migration of individuals or gametes ([link]). While some populations are fairly stable, others experience more flux. Many plants, for example, send their pollen far and wide, by wind or by bird, to pollinate other populations of the same species some distance away. Even a population that may initially appear to be stable, such as a pride of lions, can experience its fair share of immigration and emigration as developing males leave their mothers

to seek out a new pride with genetically unrelated females. This variable flow of individuals in and out of the group not only changes the gene structure of the population, but it can also introduce new genetic variation to populations in different geological locations and habitats.



Mutation

Mutations are changes to an organism’s DNA and are an important driver of diversity in populations. Species evolve because of the accumulation of mutations that occur over time. The appearance of new mutations is the most common way to introduce novel genotypic and phenotypic variance. Some mutations are unfavorable or harmful and are quickly eliminated from the population by natural selection. Others are beneficial and will spread through the population. Whether or not a mutation is beneficial or harmful is determined by whether it helps an organism survive to sexual maturity and

reproduce. Some mutations do not do anything and can linger, unaffected by natural selection, in the genome. Some can have a dramatic effect on a gene and the resulting phenotype.

Nonrandom Mating

If individuals nonrandomly mate with their peers, the result can be a changing population. There are many reasons **nonrandom mating** occurs. One reason is simple mate choice; for example, female peahens may prefer peacocks with bigger, brighter tails. Traits that lead to more matings for an individual become selected for by natural selection. One common form of mate choice, called **assortative mating**, is an individual's preference to mate with partners who are phenotypically similar to themselves.

Another cause of nonrandom mating is physical location. This is especially true in large populations spread over large geographic distances where not all individuals will have equal access to one another. Some might be miles apart through woods or over rough terrain, while others might live immediately nearby.
The sex of the American alligator (*Alligator mississippiensis*) is determined by the temperature at which the eggs are incubated. Eggs incubated at 30°C produce females, and eggs incubated at 33°C

produce males. (credit: Steve Hillebrand, USFWS)

Environmental Variance

Genes are not the only players involved in determining population variation. Phenotypes are also influenced by other factors, such as the environment ([link]). A beachgoer is likely to have darker skin than a city dweller, for example, due to regular exposure to the sun, an environmental factor. Some major characteristics, such as sex, are determined by the environment for some species. For example, some turtles and other reptiles have temperature-dependent sex determination (TSD). TSD means that individuals develop into males if their eggs are incubated within a certain temperature range, or females at a different temperature range.

Geographic separation between populations can lead to differences in the phenotypic variation between those populations. Such **geographical variation** is seen between most populations and can be significant. One type of geographic variation, called a **cline**, can be seen as populations of a given species vary gradually across an ecological gradient. Species of warm-blooded animals, for example, tend to have larger bodies in the cooler climates closer to the earth's poles, allowing them to better conserve heat. This is considered a latitudinal cline. Alternatively, flowering plants tend to bloom at different times depending on where they are along the slope of a mountain, known as an altitudinal cline.

If there is gene flow between the populations, the individuals will likely show gradual differences in phenotype along the cline. Restricted gene flow, on the other hand, can lead to abrupt differences, even speciation.

Section Summary

Both genetic and environmental factors can cause phenotypic variation in a population. Different alleles can confer different phenotypes, and different environments can also cause individuals to look or act differently. Only those differences encoded in an individual's genes, however, can be passed to its

offspring and, thus, be a target of natural selection. Natural selection works by selecting for alleles that confer beneficial traits or behaviors, while selecting against those for deleterious qualities. Genetic drift stems from the chance occurrence that some individuals in the germ line have more offspring than others. When individuals leave or join the population, allele frequencies can change as a result of gene flow. Mutations to an individual’s DNA may introduce new variation into a population. Allele frequencies can also be altered when individuals do not randomly mate with others in the group.

Art Connections

> [link] Do you think genetic drift would happen more quickly on an island or on the mainland?

> [link] Genetic drift is likely to occur more rapidly on an island where smaller populations are expected to occur.

Review Questions

When male lions reach sexual maturity, they leave their group in search of a new pride. This can alter the allele frequencies of the population through which of the following mechanisms?

1. natural selection
2. genetic drift
3. gene flow
4. random mating

C

Which of the following evolutionary forces can introduce new genetic variation into a population?

1. natural selection and genetic drift
2. mutation and gene flow
3. natural selection and nonrandom mating
4. mutation and genetic drift

B

What is assortative mating?

1. when individuals mate with those who are similar to themselves

2. when individuals mate with those who are dissimilar to themselves
3. when individuals mate with those who are the most fit in the population
4. when individuals mate with those who are least fit in the population

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A

When closely related individuals mate with each other, or inbreed, the offspring are often not as fit as the offspring of two unrelated individuals. Why?

1. Close relatives are genetically incompatible.
2. The DNA of close relatives reacts negatively in the offspring.
3. Inbreeding can bring together rare, deleterious mutations that lead to harmful phenotypes.
4. Inbreeding causes normally silent alleles to be expressed.

C

What is a cline?

1. the slope of a mountain where a population lives
2. the degree to which a mutation helps an individual survive
3. the number of individuals in the population
4. gradual geographic variation across an ecological gradient

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D

Free Response

Describe a situation in which a population would undergo the bottleneck effect and explain what impact that would have on the population’s gene pool.

A hurricane kills a large percentage of a population of sand-dwelling crustaceans—only a few individuals survive. The alleles carried by those surviving individuals would represent the entire population’s gene pool. If those surviving individuals are not representative of the original population, the post-hurricane gene pool will differ from the original gene pool.

Describe natural selection and give an example of natural selection at work in a population.

The theory of natural selection stems from the observation that some individuals in a population survive longer and have more offspring than others: thus, more of their genes are passed to the next generation. For example, a big, powerful male gorilla is much more likely than a smaller, weaker one to become the population's silverback: the pack's leader who mates far more than the other males of the group. Therefore, the pack leader will father more offspring who share half of his genes and are likely to grow bigger and stronger like their father. Over time, the genes for bigger size will increase in frequency in the population, and the average body size, as a result, grow larger on average.

Explain what a cline is and provide examples.

A cline is a type of geographic variation that is seen in populations of a given species that vary gradually across an ecological gradient. For example, warm-blooded animals tend to have larger bodies in the cooler climates closer to the earth's poles, allowing them to better conserve heat. This is considered a latitudinal cline.

Flowering plants tend to bloom at different times depending on where they are along the slope of a mountain. This is known as an altitudinal cline.

Glossary

assortative mating
: when individuals tend to mate with those who are phenotypically similar to themselves

bottleneck effect
: magnification of genetic drift as a result of natural events or catastrophes

cline
: gradual geographic variation across an ecological gradient

gene flow
: flow of alleles in and out of a population due to the migration of individuals or gametes

genetic drift
: effect of chance on a population's gene pool

genetic variance
: diversity of alleles and genotypes in a population

geographical variation

differences in the phenotypic variation between populations that are separated geographically

heritability
: fraction of population variation that can be attributed to its genetic variance

inbreeding
: mating of closely related individuals

inbreeding depression
: increase in abnormalities and disease in inbreeding populations

nonrandom mating
: changes in a population’s gene pool due to mate choice or other forces that cause individuals to mate with certain phenotypes more than others

population variation
: distribution of phenotypes in a population

selective pressure
: environmental factor that causes one phenotype to be better than another

Adaptive Evolution

By the end of this section, you will be able to:

- Explain the different ways natural selection can shape populations
- Describe how these different forces can lead to different outcomes in terms of the population variation

Natural selection only acts on the population's heritable traits: selecting for beneficial alleles and thus increasing their frequency in the population, while selecting against deleterious alleles and thereby decreasing their frequency—a process known as **adaptive evolution**. Natural selection does not act on individual alleles, however, but on entire organisms. An individual may carry a very beneficial genotype with a resulting phenotype that, for example, increases the ability to reproduce (fecundity), but if that same individual also carries an allele that results in a fatal childhood disease, that fecundity phenotype will not be passed on to the next generation because the individual will not live to reach reproductive age. Natural selection acts at the level of the individual; it selects for individuals with greater contributions to the gene pool of the next generation, known as an organism's **evolutionary (Darwinian) fitness**.

Fitness is often quantifiable and is measured by scientists in the field. However, it is not the absolute

fitness of an individual that counts, but rather how it compares to the other organisms in the population. This concept, called **relative fitness**, allows researchers to determine which individuals are contributing additional offspring to the next generation, and thus, how the population might evolve.

There are several ways selection can affect population variation: stabilizing selection, directional selection, diversifying selection, frequency-dependent selection, and sexual selection. As natural selection influences the allele frequencies in a population, individuals can either become more or less genetically similar and the phenotypes displayed can become more similar or more disparate.

Stabilizing Selection

If natural selection favors an average phenotype, selecting against extreme variation, the population will undergo **stabilizing selection** ([link]). In a population of mice that live in the woods, for example, natural selection is likely to favor individuals that best blend in with the forest floor and are less likely to be spotted by predators. Assuming the ground is a fairly consistent shade of brown, those mice whose fur is most closely matched to that color will be most likely to survive

and reproduce, passing on their genes for their brown coat. Mice that carry alleles that make them a bit lighter or a bit darker will stand out against the ground and be more likely to fall victim to predation. As a result of this selection, the population's genetic variance will decrease.

Directional Selection

When the environment changes, populations will often undergo **directional selection** ([link]), which selects for phenotypes at one end of the spectrum of existing variation. A classic example of this type of selection is the evolution of the peppered moth in eighteenth- and nineteenth-century England. Prior to the Industrial Revolution, the moths were predominately light in color, which allowed them to blend in with the light-colored trees and lichens in their environment. But as soot began spewing from factories, the trees became darkened, and the light-colored moths became easier for predatory birds to spot. Over time, the frequency of the melanic form of the moth increased because they had a higher survival rate in habitats affected by air pollution because their darker coloration blended with the sooty trees. Similarly, the hypothetical mouse population may evolve to take on a different coloration if something were to cause the forest floor where they live to change color. The result of this type of selection is a shift in the population's

genetic variance toward the new, fit phenotype.

Link to Learning

In science, sometimes things are believed to be true, and then new information comes to light that changes our understanding. The story of the peppered moth is an example: the facts behind the selection toward darker moths have recently been called into question. Read this article to learn more.

Diversifying Selection

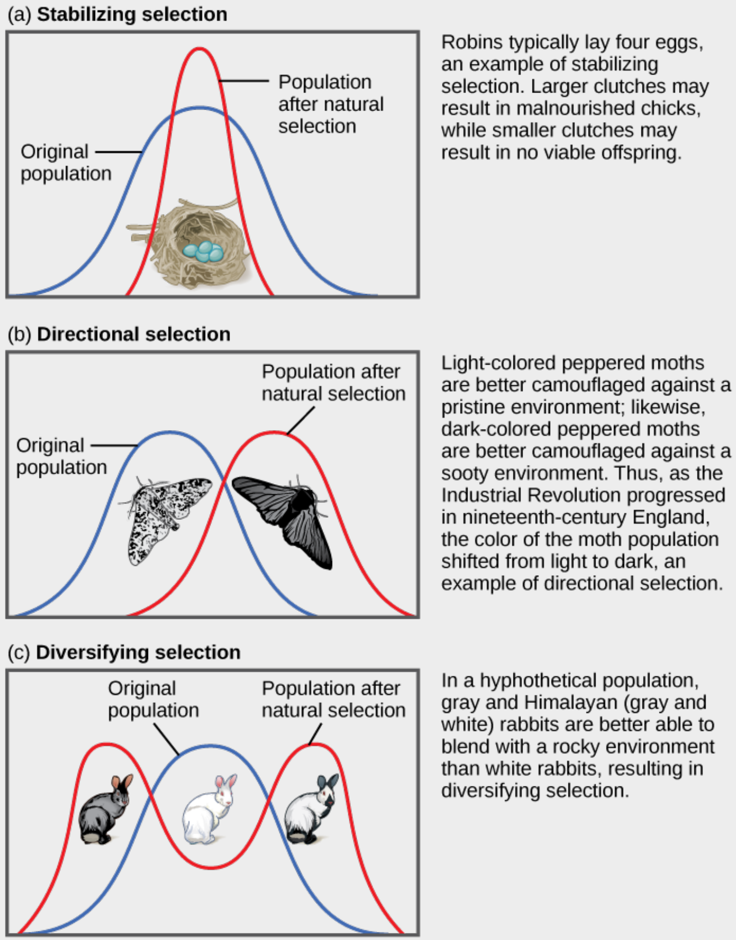
Sometimes two or more distinct phenotypes can each have their advantages and be selected for by natural selection, while the intermediate phenotypes are, on average, less fit. Known as **diversifying**

selection ([link]), this is seen in many populations of animals that have multiple male forms. Large, dominant alpha males obtain mates by brute force, while small males can sneak in for furtive copulations with the females in an alpha male’s territory. In this case, both the alpha males and the “sneaking” males will be selected for, but medium-sized males, which can’t overtake the alpha males and are too big to sneak copulations, are selected against. Diversifying selection can also occur when environmental changes favor individuals on either end of the phenotypic spectrum. Imagine a population of mice living at the beach where there is light-colored sand interspersed with patches of tall grass. In this scenario, light-colored mice that blend in with the sand would be favored, as well as dark-colored mice that can hide in the grass. Medium-colored mice, on the other hand, would not blend in with either the grass or the sand, and would thus be more likely to be eaten by predators. The result of this type of selection is increased genetic variance as the population becomes more diverse.

Art Connection

Different types of natural selection can impact the distribution of phenotypes within a population. In (a) stabilizing selection, an average phenotype is favored. In (b) directional selection, a change in

the environment shifts the spectrum of phenotypes observed. In (c) diversifying selection, two or more extreme phenotypes are selected for, while the average phenotype is selected against.



In recent years, factories have become cleaner, and less soot is released into the environment. What impact do you think this has had on the distribution of moth color in the population?

A yellow-throated side-blotched lizard is smaller than either the blue-throated or orange-throated males and appears a bit like the females of the species, allowing it to sneak copulations. (credit: “tinyfroglet”/Flickr)

Frequency-dependent Selection

Another type of selection, called **frequency-dependent selection**, favors phenotypes that are either common (positive frequency-dependent selection) or rare (negative frequency-dependent selection). An interesting example of this type of selection is seen in a unique group of lizards of the Pacific Northwest. Male common side-blotched lizards come in three throat-color patterns: orange, blue, and yellow. Each of these forms has a different reproductive strategy: orange males are the strongest and can fight other males for access to their females; blue males are medium-sized and form strong pair bonds with their mates; and yellow males ([link]) are the smallest, and look a bit like females, which allows them to sneak copulations. Like a game of rock-paper-scissors, orange beats blue, blue beats yellow, and yellow beats orange in the competition for females. That is, the big, strong orange males can fight off the blue males to mate with the blue’s pair-bonded females, the blue males are successful at guarding their mates against yellow sneaker males, and the yellow males can sneak copulations from the potential mates of the large,

polygynous orange males.

In this scenario, orange males will be favored by natural selection when the population is dominated by blue males, blue males will thrive when the population is mostly yellow males, and yellow males will be selected for when orange males are the most populous. As a result, populations of side-blotched lizards cycle in the distribution of these phenotypes—in one generation, orange might be predominant, and then yellow males will begin to rise in frequency. Once yellow males make up a majority of the population, blue males will be selected for.

Finally, when blue males become common, orange males will once again be favored.

Negative frequency-dependent selection serves to increase the population's genetic variance by selecting for rare phenotypes, whereas positive frequency-dependent selection usually decreases genetic variance by selecting for common phenotypes.

Sexual dimorphism is observed in (a) peacocks and peahens, (b) *Argiope appensa* spiders (the female spider is the large one), and in (c) wood ducks. (credit "spiders": modification of work by "Sanba38"/Wikimedia Commons; credit "duck": modification of work by Kevin Cole)

Sexual Selection

Males and females of certain species are often quite different from one another in ways beyond the reproductive organs. Males are often larger, for example, and display many elaborate colors and adornments, like the peacock's tail, while females tend to be smaller and duller in decoration. Such differences are known as **sexual dimorphisms** ([link]), which arise from the fact that in many populations, particularly animal populations, there is more variance in the reproductive success of the males than there is of the females. That is, some males—often the bigger, stronger, or more decorated males—get the vast majority of the total

matings, while others receive none. This can occur because the males are better at fighting off other males, or because females will choose to mate with the bigger or more decorated males. In either case, this variation in reproductive success generates a strong selection pressure among males to get those matings, resulting in the evolution of bigger body size and elaborate ornaments to get the females' attention. Females, on the other hand, tend to get a handful of selected matings; therefore, they are more likely to select more desirable males.

Sexual dimorphism varies widely among species, of course, and some species are even sex-role reversed. In such cases, females tend to have a greater variance in their reproductive success than males and are correspondingly selected for the bigger body size and elaborate traits usually characteristic of males.

(a) (b) (c)

The selection pressures on males and females to obtain matings is known as sexual selection; it can result in the development of secondary sexual characteristics that do not benefit the individual's likelihood of survival but help to maximize its reproductive success. Sexual selection can be so

strong that it selects for traits that are actually detrimental to the individual's survival. Think, once again, about the peacock's tail. While it is beautiful and the male with the largest, most colorful tail is more likely to win the female, it is not the most practical appendage. In addition to being more visible to predators, it makes the males slower in their attempted escapes. There is some evidence that this risk, in fact, is why females like the big tails in the first place. The speculation is that large tails carry risk, and only the best males survive that risk: the bigger the tail, the more fit the male. This idea is known as the **handicap principle**.

The **good genes hypothesis** states that males develop these impressive ornaments to show off their efficient metabolism or their ability to fight disease. Females then choose males with the most impressive traits because it signals their genetic superiority, which they will then pass on to their offspring. Though it might be argued that females should not be picky because it will likely reduce their number of offspring, if better males father more fit offspring, it may be beneficial. Fewer, healthier offspring may increase the chances of survival more than many, weaker offspring.

Link to Learning

In 1915, biologist Ronald Fisher proposed another model of sexual selection: the Fisherian runaway model, which suggests that selection of certain traits is a result of sexual preference.

In both the handicap principle and the good genes hypothesis, the trait is said to be an **honest signal** of the males' quality, thus giving females a way to find the fittest mates— males that will pass the best genes to their offspring.

No Perfect Organism

Natural selection is a driving force in evolution and can generate populations that are better adapted to survive and successfully reproduce in their environments. But natural selection cannot produce the perfect organism. Natural selection can only select on existing variation in the population; it does not create anything from scratch. Thus, it is limited by a population's existing genetic variance and whatever new alleles arise through mutation and

gene flow.

Natural selection is also limited because it works at the level of individuals, not alleles, and some alleles are linked due to their physical proximity in the genome, making them more likely to be passed on together (linkage disequilibrium). Any given individual may carry some beneficial alleles and some unfavorable alleles. It is the net effect of these alleles, or the organism's fitness, upon which natural selection can act. As a result, good alleles can be lost if they are carried by individuals that also have several overwhelmingly bad alleles; likewise, bad alleles can be kept if they are carried by individuals that have enough good alleles to result in an overall fitness benefit.

Furthermore, natural selection can be constrained by the relationships between different polymorphisms. One morph may confer a higher fitness than another, but may not increase in frequency due to the fact that going from the less beneficial to the more beneficial trait would require going through a less beneficial phenotype. Think back to the mice that live at the beach. Some are light-colored and blend in with the sand, while others are dark and blend in with the patches of grass. The dark-colored mice may be, overall, more fit than the light-colored mice, and at first glance, one might expect the light-colored mice be selected for a darker coloration. But remember that the

intermediate phenotype, a medium-colored coat, is very bad for the mice—they cannot blend in with either the sand or the grass and are more likely to be eaten by predators. As a result, the light-colored mice would not be selected for a dark coloration because those individuals that began moving in that direction (began being selected for a darker coat) would be less fit than those that stayed light.

Finally, it is important to understand that not all evolution is adaptive. While natural selection selects the fittest individuals and often results in a more fit population overall, other forces of evolution, including genetic drift and gene flow, often do the opposite: introducing deleterious alleles to the population's gene pool. Evolution has no purpose—it is not changing a population into a preconceived ideal. It is simply the sum of the various forces described in this chapter and how they influence the genetic and phenotypic variance of a population.

Section Summary

Because natural selection acts to increase the frequency of beneficial alleles and traits while decreasing the frequency of deleterious qualities, it is adaptive evolution. Natural selection acts at the level of the individual, selecting for those that have a higher overall fitness compared to the rest of the population. If the fit phenotypes are those that are

similar, natural selection will result in stabilizing selection, and an overall decrease in the population's variation. Directional selection works to shift a population's variance toward a new, fit phenotype, as environmental conditions change. In contrast, diversifying selection results in increased genetic variance by selecting for two or more distinct phenotypes.

Other types of selection include frequency-dependent selection, in which individuals with either common (positive frequency-dependent selection) or rare (negative frequency-dependent selection) are selected for. Finally, sexual selection results from the fact that one sex has more variance in the reproductive success than the other. As a result, males and females experience different selective pressures, which can often lead to the evolution of phenotypic differences, or sexual dimorphisms, between the two.

Art Connection

[link] In recent years, factories have become cleaner, and less soot is released into the environment. What impact do you think this has had on the distribution of moth color in the population?

[link] Moths have shifted to a lighter color.

Review Questions

Which type of selection results in greater genetic variance in a population?

1. stabilizing selection
2. directional selection
3. diversifying selection
4. positive frequency-dependent selection

C

When males and females of a population look or act differently, it is referred to as ______.

1. sexual dimorphism
2. sexual selection
3. diversifying selection
4. a cline

A

The good genes hypothesis is a theory that explains what?

1. why more fit individuals are more likely to have more offspring
2. why alleles that confer beneficial traits or behaviors are selected for by natural selection
3. why some deleterious mutations are maintained in the population
4. why individuals of one sex develop impressive ornamental traits

---

D

Free Response

Give an example of a trait that may have evolved as a result of the handicap principle and explain your reasoning.

The peacock's tail is a good example of the handicap principle. The tail, which makes the males more visible to predators and less able to escape, is clearly a disadvantage to the bird's survival. But because it is a disadvantage, only

the most fit males should be able to survive with it. Thus, the tail serves as an honest signal of quality to the females of the population; therefore, the male will earn more matings and greater reproductive success.

List the ways in which evolution can affect population variation and describe how they influence allele frequencies.

There are several ways evolution can affect population variation: stabilizing selection, directional selection, diversifying selection, frequency-dependent selection, and sexual selection. As these influence the allele frequencies in a population, individuals can either become more or less related, and the phenotypes displayed can become more similar or more disparate.

Glossary

adaptive evolution
: increase in frequency of beneficial alleles and decrease in deleterious alleles due to selection

directional selection
: selection that favors phenotypes at one end of the spectrum of existing variation

diversifying selection
: selection that favors two or more distinct phenotypes

evolutionary fitness
: (also, Darwinian fitness) individual’s ability to survive and reproduce

frequency-dependent selection
: selection that favors phenotypes that are either common (positive frequency-dependent selection) or rare (negative frequency-dependent selection)

good genes hypothesis
: theory of sexual selection that argues individuals develop impressive ornaments to show off their efficient metabolism or ability to fight disease

handicap principle
: theory of sexual selection that argues only the fittest individuals can afford costly traits

honest signal
: trait that gives a truthful impression of an individual’s fitness

relative fitness
: individual’s ability to survive and reproduce relative to the rest of the population

sexual dimorphism
: phenotypic difference between the males and females of a population

stabilizing selection
: selection that favors average phenotypes

Organizing Life on Earth
By the end of this section, you will be able to do the following:

- Discuss the need for a comprehensive classification system
- List the different levels of the taxonomic classification system
- Describe how systematics and taxonomy relate to phylogeny
- Discuss a phylogenetic tree's components and purpose

In scientific terms, **phylogeny** is the evolutionary history and relationship of an organism or group of organisms. A phylogeny describes the organisim's relationships, such as from which organisms it may have evolved, or to which species it is most closely related. Phylogenetic relationships provide information on shared ancestry but not necessarily on how organisms are similar or different.
Both of these phylogenetic trees show the relationship of the three domains of life—Bacteria, Archaea, and Eukarya—but the (a) rooted tree attempts to identify when various species diverged from a common ancestor while the (b) unrooted tree does not. (credit a: modification of work by Eric Gaba) A phylogenetic tree's root indicates that an ancestral lineage gave rise to all organisms on the tree. A branch point indicates where two lineages diverged. A lineage that evolved early and remains

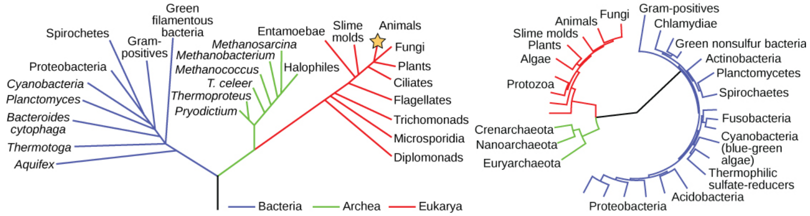
unbranched is a basal taxon. When two lineages stem from the same branch point, they are sister taxa. A branch with more than two lineages is a polytomy.

Phylogenetic Trees

Scientists use a tool called a phylogenetic tree to show the evolutionary pathways and connections among organisms. A **phylogenetic tree** is a diagram used to reflect evolutionary relationships among organisms or groups of organisms. Scientists consider phylogenetic trees to be a hypothesis of the evolutionary past since one cannot go back to confirm the proposed relationships. In other words, we can construct a “tree of life” to illustrate when different organisms evolved and to show the relationships among different organisms ([link]).

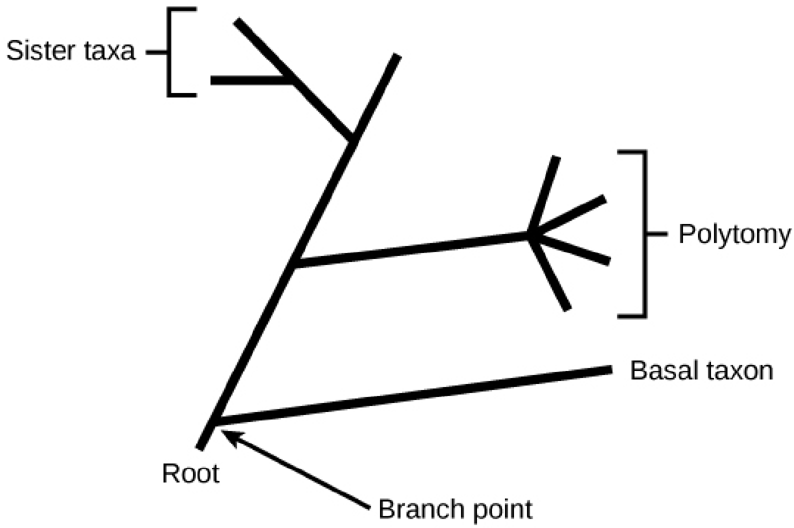
Unlike a taxonomic classification diagram, we can read a phylogenetic tree like a map of evolutionary history. Many phylogenetic trees have a single lineage at the base representing a common ancestor. Scientists call such trees **rooted**, which means there is a single ancestral lineage (typically drawn from the bottom or left) to which all organisms represented in the diagram relate. Notice in the rooted phylogenetic tree that the three domains—Bacteria, Archaea, and Eukarya—diverge from a single point and branch off. The small branch that plants and animals (including humans) occupy in

this diagram shows how recent and miniscule these groups are compared with other organisms. Unrooted trees do not show a common ancestor but do show relationships among species.



(a) Rooted phylogenetic tree (b) Unrooted phylogenetic tree

In a rooted tree, the branching indicates evolutionary relationships ([link]). The point where a split occurs, a **branch point**, represents where a single lineage evolved into a distinct new one. We call a lineage that evolved early from the root that remains unbranched a **basal taxon**. We call two lineages stemming from the same branch point **sister taxa**. A branch with more than two lineages is a **polytomy** and serves to illustrate where scientists have not definitively determined all of the relationships. Note that although sister taxa and polytomy do share an ancestor, it does not mean that the groups of organisms split or evolved from each other. Organisms in two taxa may have split at a specific branch point, but neither taxon gave rise to the other.



The diagrams above can serve as a pathway to understanding evolutionary history. We can trace the pathway from the origin of life to any individual species by navigating through the evolutionary branches between the two points. Also, by starting with a single species and tracing back towards the "trunk" of the tree, one can discover species' ancestors, as well as where lineages share a common ancestry. In addition, we can use the tree to study entire groups of organisms.

Another point to mention on phylogenetic tree structure is that rotation at branch points does not change the information. For example, if a branch point rotated and the taxon order changed, this would not alter the information because each taxon's evolution from the branch point was independent of the other.

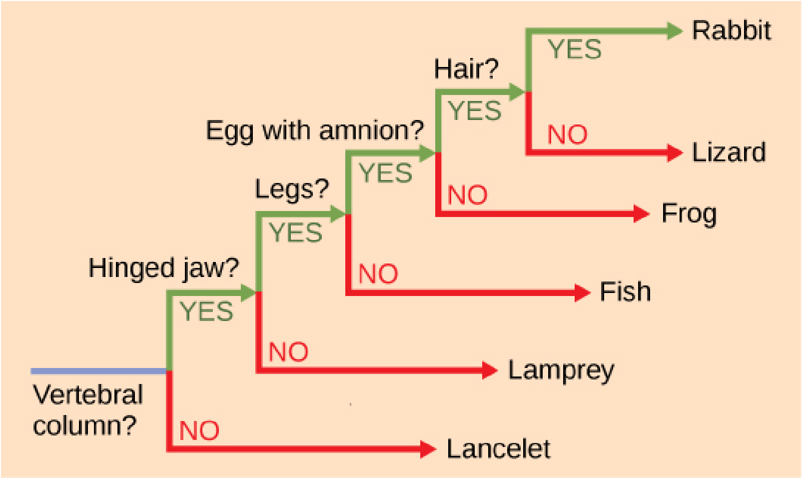
Many disciplines within the study of biology contribute to understanding how past and present life evolved over time; these disciplines together contribute to building, updating, and maintaining the “tree of life.” **Systematics** is the field that scientists use to organize and classify organisms based on evolutionary relationships. Researchers may use data from fossils, from studying the body part structures, or molecules that an organism uses, and DNA analysis. By combining data from many sources, scientists can construct an organism's phylogeny Since phylogenetic trees are hypotheses, they will continue to change as researchers discover new types of life and learn new information.

An organism that lacked a vertebral column roots this ladder-like phylogenetic tree of vertebrates. At each branch point, scientists place organisms with different characters in different groups based on shared characteristics.

Limitations of Phylogenetic Trees

It may be easy to assume that more closely related organisms look more alike, and while this is often the case, it is not always true. If two closely related lineages evolved under significantly varied surroundings, it is possible for the two groups to appear more different than other groups that are not as closely related. For example, the phylogenetic tree in [link] shows that lizards and rabbits both have amniotic eggs; whereas, frogs do not. Yet

lizards and frogs appear more similar than lizards and rabbits.



Another aspect of phylogenetic trees is that, unless otherwise indicated, the branches do not account for length of time, only the evolutionary order. In other words, a branch's length does not typically mean more time passed, nor does a short branch mean less time passed— unless specified on the diagram. For example, in [link], the tree does not indicate how much time passed between the evolution of amniotic eggs and hair. What the tree does show is the order in which things took place. Again using [link], the tree shows that the oldest trait is the vertebral column, followed by hinged jaws, and so forth. Remember that any phylogenetic tree is a part of the greater whole, and like a real tree, it does not grow in only one direction after a new branch develops. Thus, for the organisms in [link], just because a vertebral column evolved does not mean that invertebrate evolution ceased. It only means

that a new branch formed. Also, groups that are not closely related, but evolve under similar conditions, may appear more phenotypically similar to each other than to a close relative.

Link to Learning

Head to this website to see interactive exercises that allow you to explore the evolutionary relationships among species.

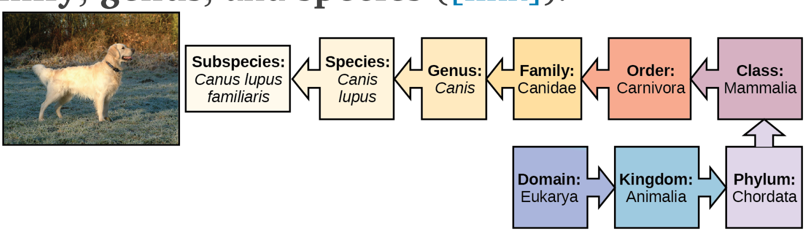
The taxonomic classification system uses a hierarchical model to organize living organisms into increasingly specific categories. The common dog, *Canis lupus familiaris*, is a subspecies of *Canis lupus*, which also includes the wolf and dingo. (credit “dog”: modification of work by Janneke Vreugdenhil)

Classification Levels

Taxonomy (which literally means “arrangement law”) is the science of classifying organisms to construct internationally shared classification systems with each organism placed into increasingly more inclusive groupings. Think about a grocery store's organization. One large space is divided into departments, such as produce, dairy, and meats.

Then each department further divides into aisles, then each aisle into categories and brands, and then finally a single product. We call this organization from larger to smaller, more specific categories a hierarchical system.

The taxonomic classification system (also called the Linnaean system after its inventor, Carl Linnaeus, a Swedish botanist, zoologist, and physician) uses a hierarchical model. Moving from the point of origin, the groups become more specific, until one branch ends as a single species. For example, after the common beginning of all life, scientists divide organisms into three large categories called domains: Bacteria, Archaea, and Eukarya. Within each domain is a second category called a **kingdom**. After kingdoms, the subsequent categories of increasing specificity are: **phylum**, **class**, **order**, **family**, **genus**, and **species** ([link]).



The kingdom Animalia stems from the Eukarya domain. [link] above shows the classification for the common dog. Therefore, the full name of an organism technically has eight terms. For the dog it is: Eukarya, Animalia, Chordata, Mammalia, Carnivora, Canidae, *Canis,* and *lupus*. Notice that each name is capitalized except for species, and the

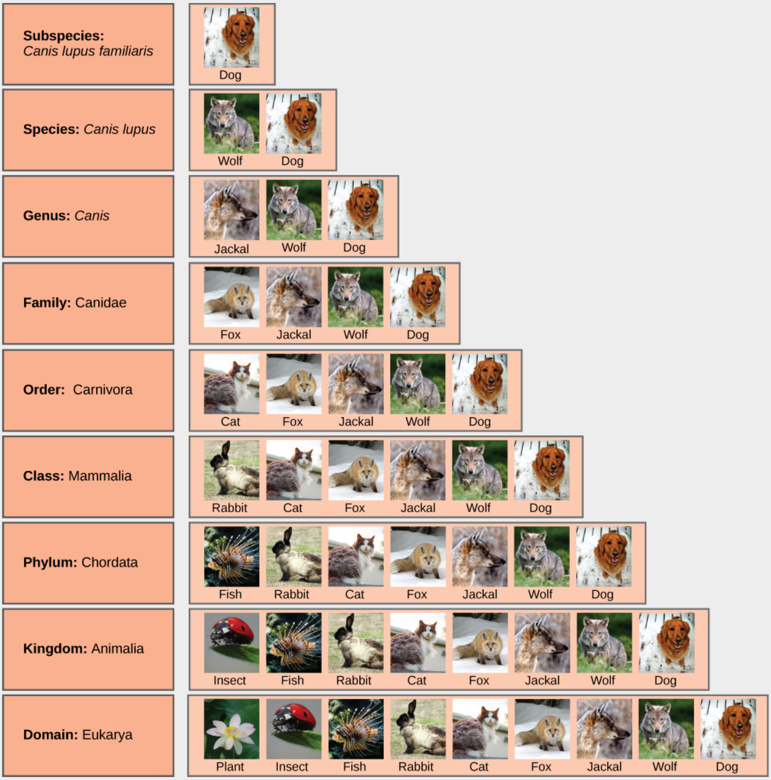
genus and species names are italicized. Scientists generally refer to an organism only by its genus and species, which is its two-word scientific name, or **binomial nomenclature**. Therefore, the scientific name of the dog is *Canis lupus*. The name at each level is also a **taxon**. In other words, dogs are in order Carnivora. Carnivora is the name of the taxon at the order level; Canidae is the taxon at the family level, and so forth. Organisms also have a common name that people typically use, in this case, dog. Note that the dog is additionally a subspecies: the "*familiaris*" in *Canis lupus familiaris.* Subspecies are members of the same species that are capable of mating and reproducing viable offspring, but they are separate subspecies due to geographic or behavioral isolation or other factors.

[link] shows how the levels move toward specificity with other organisms. Notice how the dog shares a domain with the widest diversity of organisms, including plants and butterflies. At each sublevel, the organisms become more similar because they are more closely related. Historically, scientists classified organisms using characteristics, but as DNA technology developed, they have determined more precise phylogenies.

Visual Connection

At each sublevel in the taxonomic classification

system, organisms become more similar. Dogs and wolves are the same species because they can breed and produce viable offspring, but they are different enough to be classified as different subspecies. (credit “plant”: modification of work by "berduchwal"/Flickr; credit “insect”: modification of work by Jon Sullivan; credit “fish”: modification of work by Christian Mehlführer; credit “rabbit”: modification of work by Aidan Wojtas; credit “cat”: modification of work by Jonathan Lidbeck; credit “fox”: modification of work by Kevin Bacher, NPS; credit “jackal”: modification of work by Thomas A. Hermann, NBII, USGS; credit “wolf”: modification of work by Robert Dewar; credit “dog”: modification of work by "digital_image_fan"/Flickr)



At what levels are cats and dogs part of the same group?

Link to Learning

Visit this website to explore the classifications of thousands of organisms. This reference site contains about 10% of the described species on the planet.

Recent genetic analysis and other advancements

have found that some earlier phylogenetic classifications do not align with the evolutionary past; therefore, researchers must make changes and updates as new discoveries occur. Recall that phylogenetic trees are hypotheses and are modified as data becomes available. In addition, classification historically has focused on grouping organisms mainly by shared characteristics and does not necessarily illustrate how the various groups relate to each other from an evolutionary perspective. For example, despite the fact that a hippopotamus resembles a pig more than a whale, the hippopotamus may be the whale's closest living relative.

Section Summary

Scientists continually gain new information that helps understand the evolutionary history of life on Earth. Each group of organisms went through its own evolutionary journey, or its phylogeny. Each organism shares relatedness with others, and based on morphologic and genetic evidence, scientists attempt to map the evolutionary pathways of all life on Earth. Historically, scientists organized organisms into a taxonomic classification system. However, today many scientists build phylogenetic trees to illustrate evolutionary relationships.

Visual Connection Questions

[link] At what levels are cats and dogs part of the same group?

[link] Cats and dogs are part of the same group at five levels: both are in the domain Eukarya, the kingdom Animalia, the phylum Chordata, the class Mammalia, and the order Carnivora.

Review Questions

What is used to determine phylogeny?

1. mutations
2. DNA
3. evolutionary history
4. organisms on earth

C

What do scientists in the field of systematics accomplish?

1. discover new fossil sites
2. organize and classify organisms
3. name new species
4. communicate among field biologists

B

Which statement about the taxonomic classification system is correct?

1. There are more domains than kingdoms.
2. Kingdoms are the top category of classification.
3. Classes are divisions of orders.
4. Subspecies are the most specific category of classification.

D

On a phylogenetic tree, which term refers to lineages that diverged from the same place?

1. sister taxa
2. basal taxa
3. rooted taxa
4. dichotomous taxa

A

Critical Thinking Questions

How does a phylogenetic tree relate to the passing of time?

The phylogenetic tree shows the order in which evolutionary events took place and in what order certain characteristics and organisms evolved in relation to others. It does not relate to time.

Some organisms that appear very closely related on a phylogenetic tree may not actually be closely related. Why is this?

In most cases, organisms that appear closely related actually are; however, there are cases where organisms evolved through convergence and appear closely related but are not.

List the different levels of the taxonomic classification system.

domain, kingdom, phylum, class, order, family, genus, species

Glossary

basal taxon
: branch on a phylogenetic tree that has not diverged significantly from the root ancestor

binomial nomenclature
: system of two-part scientific names for an organism, which includes genus and species names

branch point
: node on a phylogenetic tree where a single lineage splits into distinct new ones

class
: division of phylum in the taxonomic classification system

family
: division of order in the taxonomic classification system

genus
: division of family in the taxonomic classification system; the first part of the binomial scientific name

kingdom
domain division in the taxonomic classification system

order
class division in the taxonomic classification system

phylogenetic tree
diagram that reflects the evolutionary relationships among organisms or groups of organisms

phylogeny
evolutionary history and relationship of an organism or group of organisms

phylum
(plural: phyla) kingdom division in the taxonomic classification system

polytomy
branch on a phylogenetic tree with more than two groups or taxa

rooted
single ancestral lineage on a phylogenetic tree to which all organisms represented in the diagram relate

sister taxa
two lineages that diverged from the same

branch point

systematics
: field of organizing and classifying organisms based on evolutionary relationships

taxon
: (plural: taxa) single level in the taxonomic classification system

taxonomy
: science of classifying organisms

Determining Evolutionary Relationships

By the end of this section, you will be able to:

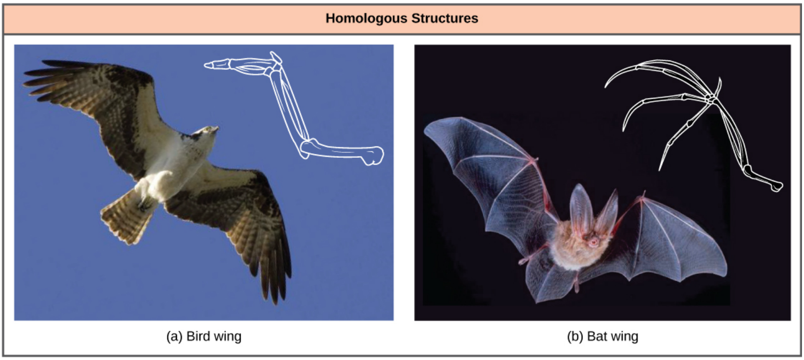
- Compare homologous and analogous traits
- Discuss the purpose of cladistics
- Describe maximum parsimony

Scientists must collect accurate information that allows them to make evolutionary connections among organisms. Similar to detective work, scientists must use evidence to uncover the facts. In the case of phylogeny, evolutionary investigations focus on two types of evidence: morphologic (form and function) and genetic.

Bat and bird wings are homologous structures, indicating that bats and birds share a common evolutionary past. (credit a: modification of work by Steve Hillebrand, USFWS; credit b: modification of work by U.S. DOI BLM) The (c) wing of a honeybee is similar in shape to a (b) bird wing and (a) bat wing, and it serves the same function. However, the honeybee wing is not composed of bones and has a distinctly different structure and embryonic origin. These wing types (insect versus bat and bird) illustrate an analogy—similar structures that do not share an evolutionary history. (credit a: modification of work by Steve Hillebrand, USFWS; credit b: modification of work by U.S. DOI BLM; credit c: modification of work by Jon Sullivan)

Two Options for Similarities

In general, organisms that share similar physical features and genomes tend to be more closely related than those that do not. Such features that overlap both morphologically (in form) and genetically are referred to as homologous structures; they stem from developmental similarities that are based on evolution. For example, the bones in the wings of bats and birds have homologous structures ([link]).



Notice it is not simply a single bone, but rather a grouping of several bones arranged in a similar way. The more complex the feature, the more likely any kind of overlap is due to a common evolutionary past. Imagine two people from different countries both inventing a car with all the same parts and in exactly the same arrangement without any previous or shared knowledge. That outcome would be highly improbable. However, if two people both invented a hammer, it would be reasonable to conclude that both could have the original idea without the help

of the other. The same relationship between complexity and shared evolutionary history is true for homologous structures in organisms.

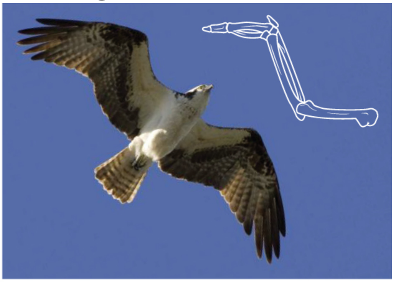
Misleading Appearances

Some organisms may be very closely related, even though a minor genetic change caused a major morphological difference to make them look quite different. Similarly, unrelated organisms may be distantly related, but appear very much alike. This usually happens because both organisms were in common adaptations that evolved within similar environmental conditions. When similar characteristics occur because of environmental constraints and not due to a close evolutionary relationship, it is called an **analogy** or homoplasy. For example, insects use wings to fly like bats and birds, but the wing structure and embryonic origin is completely different. These are called analogous structures ([link]).

Similar traits can be either homologous or analogous. Homologous structures share a similar embryonic origin; analogous organs have a similar function. For example, the bones in the front flipper of a whale are homologous to the bones in the human arm. These structures are not analogous. The wings of a butterfly and the wings of a bird are analogous but not homologous. Some structures are both analogous and homologous: the wings of a bird

and the wings of a bat are both homologous and analogous. Scientists must determine which type of similarity a feature exhibits to decipher the phylogeny of the organisms being studied.

(a) Bat wing



(b) Bird wing

(c) Insect wing

Link to Learning

This website has several examples to show how appearances can be misleading in understanding

the phylogenetic relationships of organisms.

Molecular Comparisons

With the advancement of DNA technology, the area of **molecular systematics**, which describes the use of information on the molecular level including DNA analysis, has blossomed. New computer programs not only confirm many earlier classified organisms, but also uncover previously made errors. As with physical characteristics, even the DNA sequence can be tricky to read in some cases. For some situations, two very closely related organisms can appear unrelated if a mutation occurred that caused a shift in the genetic code. An insertion or deletion mutation would move each nucleotide base over one place, causing two similar codes to appear unrelated.

Sometimes two segments of DNA code in distantly related organisms randomly share a high percentage of bases in the same locations, causing these organisms to appear closely related when they are not. For both of these situations, computer technologies have been developed to help identify the actual relationships, and, ultimately, the coupled use of both morphologic and molecular information is more effective in determining phylogeny.

Evolution Connection

Why Does Phylogeny Matter?

Evolutionary biologists could list many reasons why understanding phylogeny is important to everyday life in human society. For botanists, phylogeny acts as a guide to discovering new plants that can be used to benefit people. Think of all the ways humans use plants—food, medicine, and clothing are a few examples. If a plant contains a compound that is effective in treating cancer, scientists might want to examine all of the relatives of that plant for other useful drugs.

A research team in China identified a segment of DNA thought to be common to some medicinal plants in the family Fabaceae (the legume family) and worked to identify which species had this segment ([link]). After testing plant species in this family, the team found a DNA marker (a known location on a chromosome that enabled them to identify the species) present. Then, using the DNA to uncover phylogenetic relationships, the team could identify whether a newly discovered plant was in this family and assess its potential medicinal properties.

Dalbergia sissoo (D. sissoo) is in the Fabaceae, or legume family. Scientists found that *D. sissoo* shares a DNA marker with species within the Fabaceae family that have antifungal properties. Subsequently, *D. sissoo* was shown to have fungicidal activity, supporting the idea that DNA markers can be used to screen for plants with

potential medicinal properties.

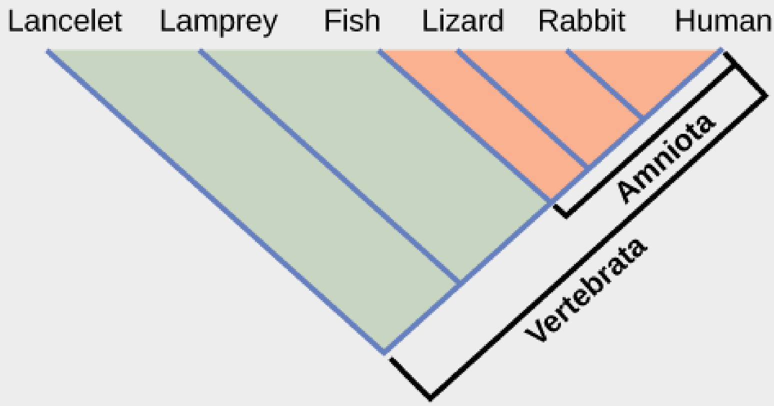
Dalbergia Sissoo, *Roxb.*

Building Phylogenetic Trees

How do scientists construct phylogenetic trees? After the homologous and analogous traits are sorted, scientists often organize the homologous traits using a system called **cladistics**. This system sorts organisms into clades: groups of organisms that descended from a single ancestor. For example, in [link], all of the organisms in the orange region evolved from a single ancestor that had amniotic eggs. Consequently, all of these organisms also have amniotic eggs and make a single clade, also called a **monophyletic group**. Clades must include all of the descendants from a branch point.

Art Connection

Lizards, rabbits, and humans all descend from a common ancestor that had an amniotic egg. Thus, lizards, rabbits, and humans all belong to the clade Amniota. Vertebrata is a larger clade that also includes fish and lamprey.



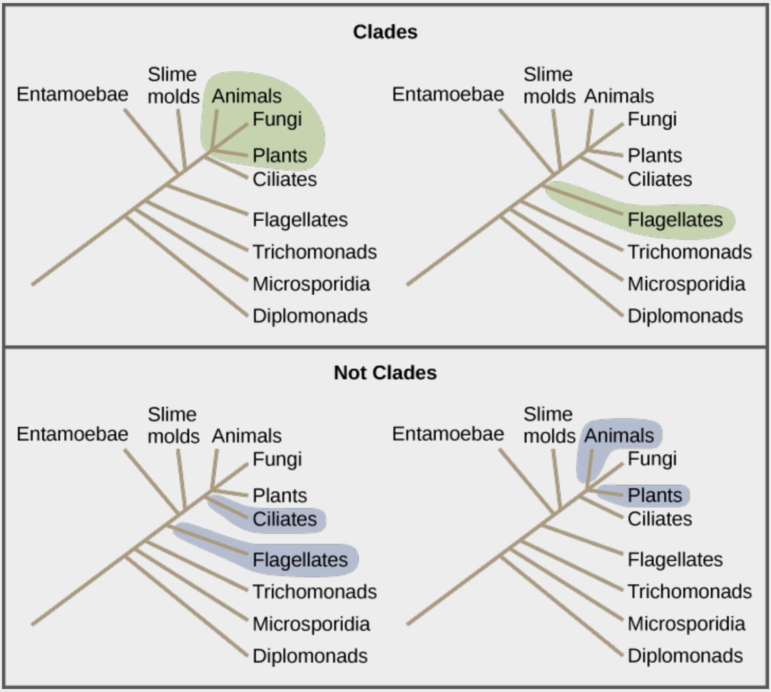
Which animals in this figure belong to a clade that includes animals with hair? Which evolved first, hair or the amniotic egg?

Clades can vary in size depending on which branch point is being referenced. The important factor is that all of the organisms in the clade or monophyletic group stem from a single point on the tree. This can be remembered because monophyletic breaks down into “mono,” meaning one, and “phyletic,” meaning evolutionary relationship. [link] shows various examples of clades. Notice how each clade comes from a single point, whereas the non-clade groups show branches that do not share a single point.

Art Connection

All the organisms within a clade stem from a single

point on the tree. A clade may contain multiple groups, as in the case of animals, fungi and plants, or a single group, as in the case of flagellates. Groups that diverge at a different branch point, or that do not include all groups in a single branch point, are not considered clades.



What is the largest clade in this diagram?

Shared Characteristics

Organisms evolve from common ancestors and then diversify. Scientists use the phrase “descent with modification” because even though related organisms have many of the same characteristics

and genetic codes, changes occur. This pattern repeats over and over as one goes through the phylogenetic tree of life:

1. A change in the genetic makeup of an organism leads to a new trait which becomes prevalent in the group.
2. Many organisms descend from this point and have this trait.
3. New variations continue to arise: some are adaptive and persist, leading to new traits.
4. With new traits, a new branch point is determined (go back to step 1 and repeat).

If a characteristic is found in the ancestor of a group, it is considered a **shared ancestral character** because all of the organisms in the taxon or clade have that trait. The vertebrate in [link] is a shared ancestral character. Now consider the amniotic egg characteristic in the same figure. Only some of the organisms in [link] have this trait, and to those that do, it is called a **shared derived character** because this trait derived at some point but does not include all of the ancestors in the tree.

The tricky aspect to shared ancestral and shared derived characters is the fact that these terms are relative. The same trait can be considered one or the other depending on the particular diagram being used. Returning to [link], note that the amniotic egg is a shared ancestral character for the Amniota

clade, while having hair is a shared derived character for some organisms in this group. These terms help scientists distinguish between clades in the building of phylogenetic trees.

Choosing the Right Relationships

Imagine being the person responsible for organizing all of the items in a department store properly—an overwhelming task. Organizing the evolutionary relationships of all life on Earth proves much more difficult: scientists must span enormous blocks of time and work with information from long-extinct organisms. Trying to decipher the proper connections, especially given the presence of homologies and analogies, makes the task of building an accurate tree of life extraordinarily difficult. Add to that the advancement of DNA technology, which now provides large quantities of genetic sequences to be used and analyzed. Taxonomy is a subjective discipline: many organisms have more than one connection to each other, so each taxonomist will decide the order of connections.

To aid in the tremendous task of describing phylogenies accurately, scientists often use a concept called **maximum parsimony**, which means that events occurred in the simplest, most obvious way. For example, if a group of people entered a forest preserve to go hiking, based on the principle

of maximum parsimony, one could predict that most of the people would hike on established trails rather than forge new ones.

For scientists deciphering evolutionary pathways, the same idea is used: the pathway of evolution probably includes the fewest major events that coincide with the evidence at hand. Starting with all of the homologous traits in a group of organisms, scientists look for the most obvious and simple order of evolutionary events that led to the occurrence of those traits.

Link to Learning

Head to this website to learn how maximum parsimony is used to create phylogenetic trees. These tools and concepts are only a few of the strategies scientists use to tackle the task of revealing the evolutionary history of life on Earth. Recently, newer technologies have uncovered surprising discoveries with unexpected relationships, such as the fact that people seem to

be more closely related to fungi than fungi are to plants. Sound unbelievable? As the information about DNA sequences grows, scientists will become closer to mapping the evolutionary history of all life on Earth.

Section Summary

To build phylogenetic trees, scientists must collect accurate information that allows them to make evolutionary connections between organisms. Using morphologic and molecular data, scientists work to identify homologous characteristics and genes. Similarities between organisms can stem either from shared evolutionary history (homologies) or from separate evolutionary paths (analogies). Newer technologies can be used to help distinguish homologies from analogies. After homologous information is identified, scientists use cladistics to organize these events as a means to determine an evolutionary timeline. Scientists apply the concept of maximum parsimony, which states that the order of events probably occurred in the most obvious and simple way with the least amount of steps. For evolutionary events, this would be the path with the least number of major divergences that correlate with the evidence.

Art Connections

[link] Which animals in this figure belong to a clade that includes animals with hair? Which evolved first, hair or the amniotic egg?

[link] Rabbits and humans belong in the clade that includes animals with hair. The amniotic egg evolved before hair because the Amniota clade is larger than the clade that encompasses animals with hair.

[link] What is the largest clade in this diagram?

[link] The largest clade encompasses the entire tree.

Review Questions

Which statement about analogies is correct?

1. They occur only as errors.

2. They are synonymous with homologous traits.
3. They are derived by similar environmental constraints.
4. They are a form of mutation.

C

What do scientists use to apply cladistics?

1. homologous traits
2. homoplasies
3. analogous traits
4. monophyletic groups

A

What is true about organisms that are a part of the same clade?

1. They all share the same basic characteristics.
2. They evolved from a shared ancestor.
3. They usually fall into the same classification taxa.
4. They have identical phylogenies.

B

Why do scientists apply the concept of maximum parsimony?

1. to decipher accurate phylogenies
2. to eliminate analogous traits
3. to identify mutations in DNA codes
4. to locate homoplasies

A

Free Response

Dolphins and fish have similar body shapes. Is this feature more likely a homologous or analogous trait?

Dolphins are mammals and fish are not, which means that their evolutionary paths (phylogenies) are quite separate. Dolphins probably adapted to have a similar body plan after returning to an aquatic lifestyle, and, therefore, this trait is probably analogous.

Why is it so important for scientists to distinguish between homologous and analogous characteristics before building phylogenetic trees?

Phylogenetic trees are based on evolutionary connections. If an analogous similarity were used on a tree, this would be erroneous and, furthermore, would cause the subsequent branches to be inaccurate.

Describe maximum parsimony.

Maximum parsimony hypothesizes that events occurred in the simplest, most obvious way, and the pathway of evolution probably includes the fewest major events that coincide with the evidence at hand.

Glossary

analogy
: (also, homoplasy) characteristic that is similar between organisms by convergent evolution, not due to the same evolutionary path

cladistics
: system used to organize homologous traits to

describe phylogenies

maximum parsimony
: applying the simplest, most obvious way with the least number of steps

molecular systematics
: technique using molecular evidence to identify phylogenetic relationships

monophyletic group
: (also, clade) organisms that share a single ancestor

shared ancestral character
: describes a characteristic on a phylogenetic tree that is shared by all organisms on the tree

shared derived character
: describes a characteristic on a phylogenetic tree that is shared only by a certain clade of organisms

Eukaryotic Origins

By the end of this section, you will be able to do the following:

- List the unifying characteristics of eukaryotes
- Describe what scientists know about the origins of eukaryotes based on the last common ancestor
- Explain the endosymbiotic theory

Organisms are classified into three domains: Archaea, Bacteria, and Eukarya. The first two lineages comprise all prokaryotic cells, and the third contains all eukaryotes. A very sparse fossil record prevents us from determining what the first members of each of these lineages looked like, so it is possible that all the events that led to the last common ancestor of extant eukaryotes will remain unknown. However, comparative biology of extant (living) organisms and the limited fossil record provide some insight into the evolution of Eukarya.

The earliest fossils found appear to be those of domain Bacteria, most likely cyanobacteria. They are about 3.5 to 3.8 billion years old and are recognizable because of their relatively complex structure and, for prokaryotes, relatively large cells. Most other prokaryotes have small cells, 1 or 2 μm in size, and would be difficult to pick out as fossils. Fossil stromatolites suggest that at least some prokaryotes lived in interactive communities, and

evidence from the structure of living eukaryotic cells suggests that it was similar ancestral interactions that gave rise to the eukaryotes. Most living eukaryotes have cells measuring 10 µm or greater. Structures this size, which might be fossilized remains of early eukaryotes, appear in the geological record in deposits dating to about 2.1 billion years ago.

Characteristics of Eukaryotes

Data from these fossils, as well as from the study of living genomes, have led comparative biologists to conclude that living eukaryotes are all descendants of a single common ancestor. Mapping the characteristics found in all major groups of eukaryotes reveals that the following characteristics are present in at least some of the members of each major lineage, or during some part of their life cycle, and therefore must have been present in the *last common ancestor*.

1. **Cells with nuclei surrounded by a nuclear envelope with nuclear pores**: This is the single characteristic that is both necessary and sufficient to define an organism as a eukaryote. All extant eukaryotes have cells with nuclei.
2. **Mitochondria**: Most extant eukaryotes have "typical" mitochondria, although some eukaryotes have very reduced mitochondrial

"remnants" and a few lack detectable mitochondria.
3. **Cytoskeleton of microtubules and microfilaments**: Eukaryotic cells possess the structural and motility components called *actin microfilaments and microtubules*. All extant eukaryotes have these cytoskeletal elements.
4. **Flagella and cilia**: Organelles associated with cell motility. Some extant eukaryotes lack flagella and/or cilia, but their presence in related lineages suggests that they are descended from ancestors that possessed these organelles.
5. **Chromosomes organized by histones**: Each eukaryotic chromosome consists of a linear DNA molecule coiled around basic (alkaline) proteins called histones. The few eukaryotes with chromosomes lacking histones clearly evolved from ancestors that had them.
6. **Mitosis**: A process of nuclear division in which replicated chromosomes are divided and separated using elements of the cytoskeleton. Mitosis is universally present in eukaryotes.
7. **Sexual reproduction**: A meiotic process of nuclear division and genetic recombination unique to eukaryotes. During this process, diploid nuclei at one stage of the life cycle undergo meiosis to yield haploid nuclei, which subsequently fuse together (karyogamy) to create a diploid zygote nucleus.
8. **Cell walls**: It might be reasonable to conclude

that the last common ancestor could make cell walls during some stage of its life cycle, simple because cell walls were present in their prokaryote precursors. However, not enough is known about eukaryotes' cell walls and their development to know how much homology exists between those of prokaryotes and eukaryotes. If the last common ancestor could make cell walls, it is clear that this ability must have been lost in many groups.

Mitochondria. In this transmission electron micrograph of mitochondria in a mammalian lung cell, the cristae, infoldings of the mitochondrial inner membrane, can be seen in cross-section. (credit: Louise Howard) Chloroplasts. (a) This chloroplast cross-section illustrates its elaborate inner membrane organization. Stacks of thylakoid membranes compartmentalize photosynthetic enzymes and provide scaffolding for chloroplast DNA. (b) In this micrograph of *Elodea* sp., the chloroplasts can be seen as small green spheres. (credit b: modification of work by Brandon Zierer; scale-bar data from Matt Russell) Algae. (a) Red algae and (b) green algae (seen here by light microscopy) share similar DNA sequences with photosynthetic cyanobacteria. Scientists speculate that, in a process called endosymbiosis, an ancestral prokaryote engulfed a photosynthetic cyanobacterium that evolved into modern-day chloroplasts. (credit a: modification of work by Ed

Bierman; credit b: modification of work by G. Fahnenstiel, NOAA; scale-bar data from Matt Russell)

Endosymbiosis and the Evolution of Eukaryotes

Before we discuss the origins of eukaryotes, it is first important to understand that all extant eukaryotes are likely the descendants of a chimera-like organism that was a composite of a host cell and the cell(s) of an alpha-proteobacterium that “took up residence” inside it. This major theme in the origin of eukaryotes is known as **endosymbiosis**, one cell engulfing another such that the engulfed cell survives and both cells benefit. Over many generations, a symbiotic relationship can result in two organisms that depend on each other so completely that neither could survive on its own. Endosymbiotic events likely contributed to the origin of the last common ancestor of today’s eukaryotes and to later diversification in certain lineages of eukaryotes ([link]). Similar endosymbiotic associations are not uncommon in living eukaryotes. Before explaining this further, it is necessary to consider metabolism in prokaryotes.

Prokaryotic Metabolism

Many important metabolic processes arose in

prokaryotes; however, some of these processes, such as nitrogen fixation, are never found in eukaryotes. The process of aerobic respiration is found in all major lineages of eukaryotes, and it is localized in the mitochondria. Aerobic respiration is also found in many lineages of prokaryotes, but it is not present in all of them, and a great deal of evidence suggests that such anaerobic prokaryotes never carried out aerobic respiration nor did their ancestors.

While today's atmosphere is about 20 percent molecular oxygen (O_2), geological evidence shows that it originally lacked O_2. Without oxygen, aerobic respiration would not be expected, and living things would have relied on anaerobic respiration or the process of fermentation instead. At some point before about 3.8 billion years ago, some prokaryotes began using energy from sunlight to power anabolic processes that reduce carbon dioxide to form organic compounds. That is, they evolved the ability to photosynthesize. Hydrogen, derived from various sources, was "captured" using light-powered reactions to reduce fixed carbon dioxide in the Calvin cycle. The group of Gram-negative bacteria that gave rise to cyanobacteria used water as the hydrogen source and released O_2 as a "waste" product.

Eventually, the amount of photosynthetic oxygen built up in some environments to levels that posed a risk to living organisms, since it can damage many

organic compounds. Various metabolic processes evolved that protected organisms from oxygen, one of which, aerobic respiration, also generated high levels of ATP. It became widely present among prokaryotes, including in a free-living group we now call alpha-proteobacteria. Organisms that did not acquire aerobic respiration had to remain in oxygen-free environments. Originally, oxygen-rich environments were likely localized around places where cyanobacteria were abundant and active, but by about 2 billion years ago, geological evidence shows that oxygen was building up to higher concentrations in the atmosphere. Oxygen levels similar to today's levels only arose within the last 700 million years.

Recall that the first fossils that we believe to be eukaryotes date to about 2 billion years old, so they seemed to have evolved and diversified rapidly as oxygen levels were increasing. Also, recall that all extant eukaryotes descended from an ancestor with mitochondria. These organelles were first observed by light microscopists in the late 1800s, where they appeared to be somewhat worm-shaped structures that seemed to be moving around in the cell. Some early observers suggested that they might be bacteria living inside host cells, but these hypotheses remained unknown or rejected in most scientific communities.

Endosymbiotic Theory

As cell biology developed in the twentieth century, it became clear that mitochondria were the organelles responsible for producing ATP using aerobic respiration, in which oxygen was the final electron acceptor. In the 1960s, American biologist Lynn Margulis of Boston University developed the **endosymbiotic theory**, which states that eukaryotes may have been a product of one cell engulfing another, one living within another, and coevolving over time until the separate cells were no longer recognizable as such and shared genetic control of a mutualistic metabolic pathway to produce ATP. In 1967, Margulis introduced new data to support her work on the theory and substantiated her findings through microbiological evidence. Although Margulis's work initially was met with resistance, this basic component of this once-revolutionary hypothesis is now widely accepted, with work progressing on uncovering the steps involved in this evolutionary process and the key players involved.

While the metabolic organelles and genes responsible for many energy-harvesting processes appear to have had their origins in bacteria, our nuclear genes and the molecular machinery responsible for replication and expression appear to be more closely related to those found in the Archaea. Much remains to be clarified about how this relationship occurred; this continues to be an exciting field of discovery in biology. For instance, it

is *not* known whether the endosymbiotic event that led to mitochondria occurred before or after the host cell had a nucleus. Such organisms would be among the extinct precursors of the last common ancestor of eukaryotes.

Mitochondria

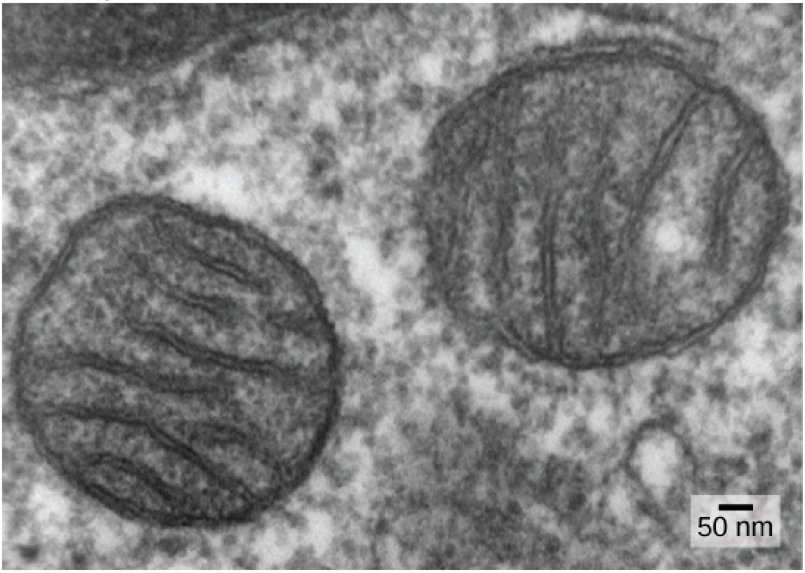
One of the major features distinguishing prokaryotes from eukaryotes is the presence of mitochondria, or their reduced derivatives, in virtually all eukaryotic cells. Eukaryotic cells may contain anywhere from one to several thousand mitochondria, depending on the cell's level of energy consumption, in humans being most abundant in the liver and skeletal muscles. Each mitochondrion measures 1 to 10 or greater micrometers in length and exists in the cell as an organelle that can be ovoid to worm-shaped to intricately branched ([link]). However, although they may have originated as free-living aerobic organisms, mitochondria can no longer survive and reproduce outside the cell.

Mitochondria have several features that suggest their relationship to alpha-proteobacteria ([link]). Alpha-proteobacteria are a large group of bacteria that includes species symbiotic with plants, disease organisms that can infect humans via ticks, and many free-living species that use light for energy. Mitochondria have their own genomes, with a circular chromosome stabilized by attachments to

the inner membrane. Mitochondria also have special ribosomes and transfer RNAs that resemble these same components in prokaryotes. An intriguing feature of mitochondria is that many of them exhibit minor differences from the universal genetic code. However, many of the genes for respiratory proteins are now relocated in the nucleus. When these genes are compared to those of other organisms, they appear to be of alpha-proteobacterial origin. In some eukaryotic groups, such genes are found in the mitochondria, whereas in other groups, they are found in the nucleus. This has been interpreted as evidence that over evolutionary time, genes have been transferred from the endosymbiont chromosome to those of the host genome. This apparent "loss" of genes by the endosymbiont is probably one explanation why mitochondria cannot live without a host.

Another line of evidence supporting the idea that mitochondria were derived by endosymbiosis comes from the structure of the mitochondrian itself. Most mitochondria are shaped like alpha-proteobacteria and are surrounded by two membranes; the inner membrane is bacterial in nature whereas the outer membrane is eukaryotic in nature. This is exactly what one would expect if one membrane-bound organism was engulfed into a vacuole by another membrane-bound organism. The outer mitochondrial membrane was derived by the enclosing vesicle, while the inner membrane was

derived from the plasma membrane of the endosymbiont. The mitochondrial inner membrane is extensive and involves substantial infoldings called **cristae** that resemble the textured, outer surface of alpha-proteobacteria. The matrix and inner membrane are rich with the enzymes necessary for aerobic respiration.



The third line of evidence comes from the production of new mitochondria. Mitochondria divide independently by a process that resembles binary fission in prokaryotes. Mitochondria arise only from previous mitochondria; they are not formed from scratch (de novo) by the eukaryotic cell. Mitochondria may fuse together; and they may be moved around inside the cell by interactions with the cytoskeleton. They reproduce within their enclosing cell and are distributed with the cytoplasm when a cell divides or two cells fuse.

Therefore, although these organelles are highly integrated into the eukaryotic cell, they still reproduce as if they were independent organisms within the cell. However, their reproduction is synchronized with the activity and division of the cell. These features all support the theory that mitochondria were once free-living prokaryotes.

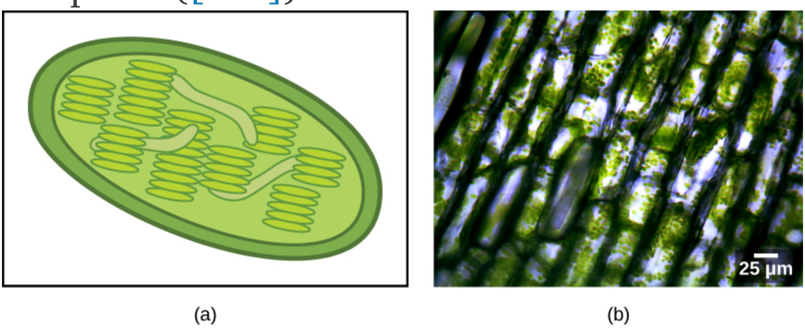
Some living eukaryotes are anaerobic and cannot survive in the presence of too much oxygen. However, a few appear to lack organelles that could be recognized as mitochondria. In the 1970s and on into the early 1990s, many biologists suggested that some of these eukaryotes were descended from ancestors whose lineages had diverged from the lineage of mitochondrion-containing eukaryotes before endosymbiosis occurred. Later findings suggest that *reduced organelles* are found in most, if not all, anaerobic eukaryotes, and that virtually all eukaryotes appear to carry some genes in their nuclei that are of mitochondrial origin.

In addition to the aerobic generation of ATP, mitochondria have several other metabolic functions. One of these functions is to generate clusters of iron and sulfur that are important cofactors of many enzymes. Such functions are often associated with the reduced mitochondrion-derived organelles of anaerobic eukaryotes. The protist *Monocercomonoides,* an inhabitant of vertebrate digestive tracts, appears to be an exception; it has

no mitochondria and its genome contains neither genes derived from mitochondria nor nuclear genes related to mitochondrial maintenance. However, it is related to other protists with reduced mitochondria and probably represents an end-point in mitochondrial reduction. Although most biologists accept that the last common ancestor of eukaryotes had mitochondria, it appears that the complex relationship between mitochondria and their host cell continues to evolve.

Plastids

Some groups of eukaryotes are photosynthetic. Their cells contain, in addition to the standard eukaryotic organelles, another kind of organelle called a **plastid**. When such cells are carrying out photosynthesis, their plastids are rich in the pigment chlorophyll *a* and a range of other pigments, called *accessory pigments*, which are involved in harvesting energy from light. Photosynthetic plastids are called chloroplasts ([link]).



Like mitochondria, plastids appear to have an

endosymbiotic origin. This hypothesis was also proposed and championed with the first direct evidence by Lynn Margulis. We now know that plastids are derived from cyanobacteria that lived inside the cells of an ancestral, aerobic, heterotrophic eukaryote. This is called primary endosymbiosis, and plastids of primary origin are surrounded by two membranes. However, the best evidence is that the acquisition of cyanobacterial endosymbionts has happened *twice* in the history of eukaryotes. In one case, the common ancestor of the major lineage/supergroup Archaeplastida took on a cyanobacterial endosymbiont; in the other, the ancestor of the small amoeboid rhizarian taxon, *Paulinella*, took on a different cyanobacterial endosymbiont. Almost all photosynthetic eukaryotes are descended from the first event, and only a couple of species are derived from the other, which in evolutionary terms, appears to be more recent.

Cyanobacteria are a group of Gram-negative bacteria with all the conventional structures of the group. However, unlike most prokaryotes, they have extensive, internal membrane-bound sacs called thylakoids. Chlorophyll is a component of these membranes, as are many of the proteins of the light reactions of photosynthesis. Cyanobacteria also have the peptidoglycan wall and lipopolysaccharide layer associated with Gram-negative bacteria.

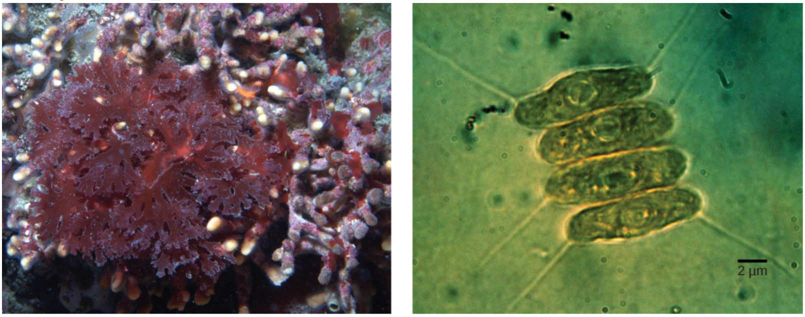
Chloroplasts of primary endosymbiotic origin have

thylakoids, a circular DNA chromosome, and ribosomes similar to those of cyanobacteria. As in mitochondria, each chloroplast is surrounded by two membranes. The outer membrane is thought to be derived from the enclosing vacuole of the host, and the inner membrane is thought to be derived from the plasma membrane of the cyanobacterial endosymbiont. In the group of Archaeplastida called the glaucophytes and in the rhizarian *Paulinella*, a thin peptidoglycan layer is still present between the outer and inner plastid membranes. All other plastids lack this relict of the cyanobacterial wall.

There is also, as with the case of mitochondria, strong evidence that many of the genes of the endosymbiont were transferred to the nucleus. Plastids, like mitochondria, cannot live independently outside the host. In addition, like mitochondria, plastids are derived from the division of other plastids and never built from scratch. Researchers have suggested that the endosymbiotic event that led to Archaeplastida occurred 1 to 1.5 billion years ago, at least 5 hundred million years after the fossil record suggests that eukaryotes were present.

Not all plastids in eukaryotes are derived directly from primary endosymbiosis. Some of the major groups of algae became photosynthetic by secondary endosymbiosis, that is, by taking in either green algae or red algae (both from Archaeplastida) as

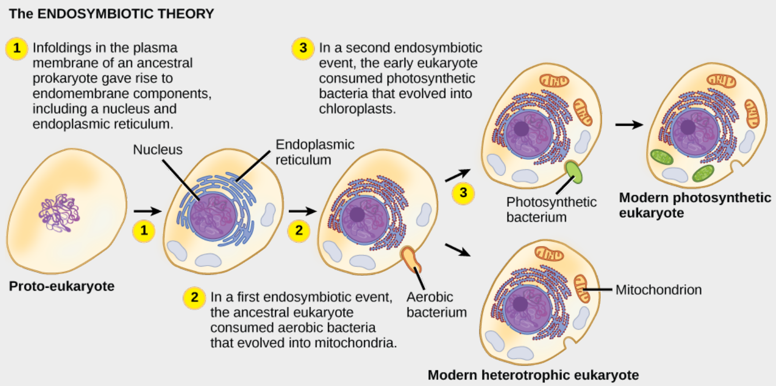
endosymbionts ([link]). Numerous microscopic and genetic studies have supported this conclusion. Secondary plastids are surrounded by three or more membranes, and some secondary plastids even have clear remnants of the nucleus (nucleomorphs) of endosymbiotic algae. There are even cases where tertiary or higher-order endosymbiotic events are the best explanations for the features of some eukaryotic plastids.



(a) (b)

Visual Connection

The Endosymbiotic Theory. The first eukaryote may have originated from an ancestral prokaryote that had undergone membrane proliferation, compartmentalization of cellular function (into a nucleus, lysosomes, and an endoplasmic reticulum), and the establishment of endosymbiotic relationships with an aerobic prokaryote, and, in some cases, a photosynthetic prokaryote, to form mitochondria and chloroplasts, respectively.



What evidence is there that mitochondria were incorporated into the ancestral eukaryotic cell before chloroplasts?

Evolution Connection

Secondary Endosymbiosis in Chlorarachniophytes

Endosymbiosis involves one cell engulfing another to produce, over time, a coevolved relationship in which neither cell could survive alone. The chloroplasts of red and green algae, for instance, are derived from the engulfment of a photosynthetic cyanobacterium by an ancestral prokaryote.

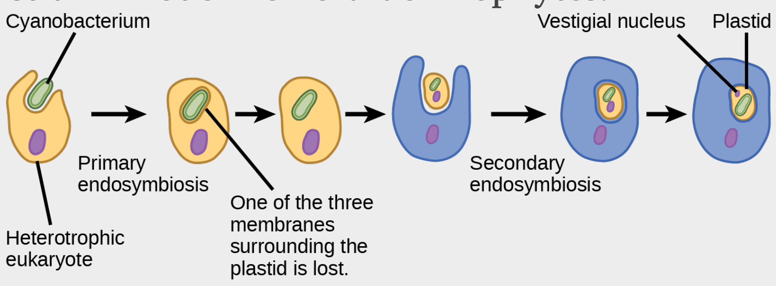
This evidence suggests the possibility that an ancestral cell (already containing a photosynthetic endosymbiont) was engulfed by another eukaryote cell, resulting in a secondary endosymbiosis.

Molecular and morphological evidence suggest that the *chlorarachniophyte protists* are derived from a secondary endosymbiotic event.

Chlorarachniophytes are rare algae indigenous to

tropical seas and sand. They are classified into the Rhizarian supergroup. Chlorarachniophytes are reticulose amoebae, extending thin cytoplasmic strands that interconnect them with other chlorarachniophytes in a cytoplasmic network. These protists are thought to have originated when a eukaryote engulfed a green alga, the latter of which had previously established an endosymbiotic relationship with a photosynthetic cyanobacterium ([link]).

Secondary endosymbiosis. The hypothesized process of several endosymbiotic events leading to the evolution of chlorarachniophytes is shown. In a primary endosymbiotic event, a heterotrophic eukaryote consumed a cyanobacterium. In a secondary endosymbiotic event, the cell resulting from primary endosymbiosis was consumed by a second cell. The resulting organelle became a plastid in modern chlorarachniophytes.



Several lines of evidence support that chlorarachniophytes evolved from secondary endosymbiosis. The chloroplasts contained within the green algal endosymbionts still are capable of photosynthesis, making chlorarachniophytes photosynthetic. The green algal endosymbiont also

exhibits a vestigial nucleus. In fact, it appears that chlorarachniophytes are the products of an evolutionarily recent secondary endosymbiotic event. The plastids of chlorarachniophytes are surrounded by *four membranes*: The first two correspond to the inner and outer membranes of the photosynthetic cyanobacterium, the third corresponds to plasma membrane of the green alga, and the fourth corresponds to the vacuole that surrounded the green alga when it was engulfed by the chlorarachniophyte ancestor. In other lineages that involved secondary endosymbiosis, only *three membranes* can be identified around plastids. This is currently interpreted as a sequential loss of a membrane during the course of evolution.

The process of secondary endosymbiosis is not unique to chlorarachniophytes. Secondary plastids are also found in the Excavates and the Chromalveolates. In the Excavates, secondary endosymbiosis of green algae led to euglenid protists, while in the Chromalveolates, secondary endosymbiosis of red algae led to the evolution of plastids in dinoflagellates, apicomplexans, and stramenopiles.

Section Summary

The oldest fossil evidence of eukaryotes is about 2 billion years old. Fossils older than this all appear to be prokaryotes. It is probable that today's eukaryotes are descended from an ancestor that had a prokaryotic organization. The last common ancestor of today's Eukarya had several characteristics, including cells with nuclei and an endomembrane system (which includes the nuclear envelope). Its chromosomes were linear and contained DNA associated with histones. The nuclear genome seems to be descended from an archaean ancestor. This ancestor would have had a cytoskeleton and divided its chromosomes mitotically.

The ancestral cytoskeletal system included the ability to make cilia/flagella during at least part of its life cycle. It was aerobic because it had mitochondria derived from an aerobic alpha-proteobacterium that lived inside a host cell. Whether this host had a nucleus at the time of the initial symbiosis remains unknown. The last common ancestor may have had a cell wall for at least part of its life cycle, but more data are needed to confirm this hypothesis. Today's eukaryotes are very diverse in their shapes, organization, life cycles, and number of cells per individual.

Visual Connection Questions

[link] What evidence is there that mitochondria were incorporated into the ancestral eukaryotic cell before chloroplasts?

[link] All eukaryotic cells have mitochondria, but not all eukaryotic cells have chloroplasts.

Review Questions

What event is thought to have contributed to the evolution of eukaryotes?

1. global warming
2. glaciation
3. volcanic activity
4. oxygenation of the atmosphere

D

Which characteristic is shared by prokaryotes and eukaryotes?

1. cytoskeleton
2. nuclear envelope
3. DNA-based genome

4. mitochondria

C

Mitochondria most likely evolved by _________.

1. a photosynthetic cyanobacterium
2. cytoskeletal elements
3. endosymbiosis
4. membrane proliferation

C

Which of these protists is believed to have evolved following a secondary endosymbiosis?

1. green algae
2. cyanobacteria
3. red algae
4. chlorarachniophytes

D

In 2016, scientists published the genome of *Monocercomonoides*, and demonstrated that this organism has no detectable mitochondrial

genes. However, its genome was arranged in linear chromosomes wrapped around histones which are contained within the nucleus. *Monocercomonoides* is therefore a(n) ______.

1. Bacteria
2. Archea
3. Eukaryote
4. Endosymbiont

C

Which of the following observations about a bacterium would distinguish it from the last eukaryotic common ancestor?

1. A double-stranded DNA genome
2. Lack of a membrane-bound structure surrounding the genome
3. Fatty acids in the lipid bilayer of the plasma membrane
4. Enclosed by a cell wall

B

Critical Thinking Questions

Describe the hypothesized steps in the origin of eukaryotic cells.

Eukaryotic cells arose through endosymbiotic events that gave rise to the energy-producing organelles within the eukaryotic cells such as mitochondria and chloroplasts. The nuclear genome of eukaryotes is related most closely to the Archaea, so it may have been an early archaean that engulfed a bacterial cell that evolved into a mitochondrion. Mitochondria appear to have originated from an alpha-proteobacterium, whereas chloroplasts originated as a cyanobacterium. There is also evidence of secondary endosymbiotic events. Other cell components may also have resulted from endosymbiotic events.

Some aspects of eukaryotes are more similar to Archaea, while other aspects of eukaryotic cell composition appear more closely related to Bacteria. Explain how endosymbiosis could resolve this paradox.

The endosymbiotic theory proposes that one organism engulfed another, and the two co-evolved together until they could not exist independently. If a bacterium engulfed an archaeon, or vice versa, and the two developed

an obligate symbiotic relationship, the resulting eukaryote thousands of years later would retain features from both original cells.

Glossary

endosymbiosis
: engulfment of one cell within another such that the engulfed cell survives, and both cells benefit; the process responsible for the evolution of mitochondria and chloroplasts in eukaryotes

endosymbiotic theory
: theory that states that eukaryotes may have been a product of one cell engulfing another, one living within another, and evolving over time until the separate cells were no longer recognizable as such

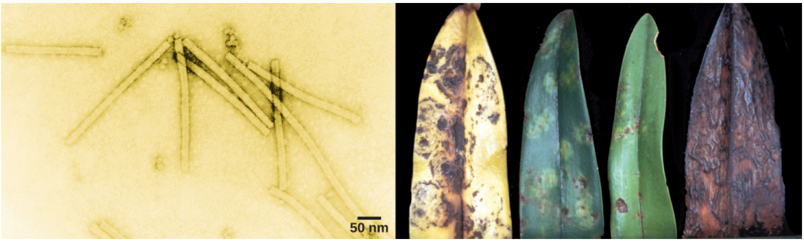
plastid
: one of a group of related organelles in plant cells that are involved in the storage of starches, fats, proteins, and pigments

Viruses
By the end of this section, you will be able to:

- Describe how viruses were first discovered and how they are detected
- Discuss three hypotheses about how viruses evolved
- Recognize the basic shapes of viruses
- List the steps of replication and explain what occurs at each step

The tobacco mosaic virus (left), seen here by transmission electron microscopy, was the first virus to be discovered. The virus causes disease in tobacco and other plants, such as the orchid (right). (credit a: USDA ARS; credit b: modification of work by USDA Forest Service, Department of Plant Pathology Archive North Carolina State University; scale-bar data from Matt Russell)

Introduction



No one knows exactly when viruses emerged or from where they came, since viruses do not leave

historical footprints such as fossils. Modern viruses are thought to be a mosaic of bits and pieces of nucleic acids picked up from various sources along their respective evolutionary paths. Viruses are acellular, parasitic entities that are not classified within any kingdom. Unlike most living organisms, viruses are not cells and cannot divide. Instead, they infect a host cell and use the host's replication processes to produce identical progeny virus particles. Viruses infect organisms as diverse as bacteria, plants, and animals. They exist in a netherworld between a living organism and a nonliving entity. Living things grow, metabolize, and reproduce. Viruses replicate, but to do so, they are entirely dependent on their host cells. They do not metabolize or grow, but are assembled in their mature form.

Viruses are diverse entities. They vary in their structure, their replication methods, and in their target hosts. Nearly all forms of life—from bacteria and archaea to eukaryotes such as plants, animals, and fungi—have viruses that infect them. While most biological diversity can be understood through evolutionary history, such as how species have adapted to conditions and environments, much about virus origins and evolution remains unknown. In these transmission electron micrographs, (a) a virus is dwarfed by the bacterial cell it infects, while (b) these *E. coli* cells are dwarfed by cultured colon cells. (credit a: modification of work by U.S. Dept.

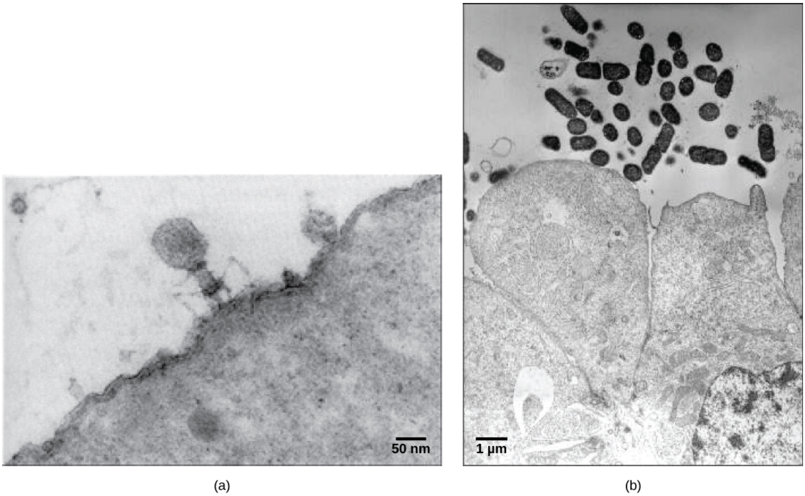
of Energy, Office of Science, LBL, PBD; credit b: modification of work by J.P. Nataro and S. Sears, unpub. data, CDC; scale-bar data from Matt Russell)

Discovery and Detection

Viruses were first discovered after the development of a porcelain filter, called the Chamberland-Pasteur filter, which could remove all bacteria visible in the microscope from any liquid sample. In 1886, Adolph Meyer demonstrated that a disease of tobacco plants, tobacco mosaic disease, could be transferred from a diseased plant to a healthy one via liquid plant extracts. In 1892, Dmitri Ivanowski showed that this disease could be transmitted in this way even after the Chamberland-Pasteur filter had removed all viable bacteria from the extract. Still, it was many years before it was proven that these "filterable" infectious agents were not simply very small bacteria but were a new type of very small, disease-causing particle.

Virions, single virus particles, are very small, about 20–250 nanometers in diameter. These individual virus particles are the infectious form of a virus outside the host cell. Unlike bacteria (which are about 100-times larger), we cannot see viruses with a light microscope, with the exception of some large virions of the poxvirus family. It was not until the development of the electron microscope in the late 1930s that scientists got their first good view of the

structure of the tobacco mosaic virus (TMV) ([link]) and other viruses ([link]). The surface structure of virions can be observed by both scanning and transmission electron microscopy, whereas the internal structures of the virus can only be observed in images from a transmission electron microscope. The use of these technologies has allowed for the discovery of many viruses of all types of living organisms. They were initially grouped by shared morphology. Later, groups of viruses were classified by the type of nucleic acid they contained, DNA or RNA, and whether their nucleic acid was single- or double-stranded. More recently, molecular analysis of viral replicative cycles has further refined their classification.



Evolution of Viruses

Although biologists have accumulated a significant

amount of knowledge about how present-day viruses evolve, much less is known about how viruses originated in the first place. When exploring the evolutionary history of most organisms, scientists can look at fossil records and similar historic evidence. However, viruses do not fossilize, so researchers must conjecture by investigating how today's viruses evolve and by using biochemical and genetic information to create speculative virus histories.

While most findings agree that viruses don't have a single common ancestor, scholars have yet to find a single hypothesis about virus origins that is fully accepted in the field. One such hypothesis, called devolution or the regressive hypothesis, proposes to explain the origin of viruses by suggesting that viruses evolved from free-living cells. However, many components of how this process might have occurred are a mystery. A second hypothesis (called escapist or the progressive hypothesis) accounts for viruses having either an RNA or a DNA genome and suggests that viruses originated from RNA and DNA molecules that escaped from a host cell. A third hypothesis posits a system of self-replication similar to that of other self-replicating molecules, likely evolving alongside the cells they rely on as hosts; studies of some plant pathogens support this hypothesis.

As technology advances, scientists may develop and

refine further hypotheses to explain the origin of viruses. The emerging field called virus molecular systematics attempts to do just that through comparisons of sequenced genetic material. These researchers hope to one day better understand the origin of viruses, a discovery that could lead to advances in the treatments for the ailments they produce.

Viral Morphology

Viruses are **acellular**, meaning they are biological entities that do not have a cellular structure. They therefore lack most of the components of cells, such as organelles, ribosomes, and the plasma membrane. A virion consists of a nucleic acid core, an outer protein coating or capsid, and sometimes an outer **envelope** made of membranes derived from the host cell. Viruses may also contain additional proteins, such as enzymes. The most obvious difference between members of viral families is their morphology, which is quite diverse. An interesting feature of viral complexity is that the complexity of the host does not correlate with the complexity of the virion. Some of the most complex virion structures are observed in bacteriophages, viruses that infect the simplest living organisms, bacteria.

Morphology

Viruses come in many shapes and sizes, but these are consistent and distinct for each viral family. All virions have a nucleic acid genome covered by a protective layer of proteins, called a **capsid**. The capsid is made up of protein subunits called **capsomeres**. Some viral capsids are simple polyhedral "spheres," whereas others are quite complex in structure.

In general, the shapes of viruses are classified into four groups: filamentous, isometric (or icosahedral), enveloped, and head and tail. Filamentous viruses are long and cylindrical. Many plant viruses are filamentous, including TMV. Isometric viruses have shapes that are roughly spherical, such as poliovirus or herpesviruses. Enveloped viruses have membranes surrounding capsids. Animal viruses, such as HIV, are frequently enveloped. Head and tail viruses infect bacteria and have a head that is similar to icosahedral viruses and a tail shape like filamentous viruses.

Many viruses use some sort of protein to attach to their host cells via molecules on the cell called **viral receptors** For these viruses, attachment is a requirement for later penetration of the cell membrane, so they can complete their replication inside the cell. The receptors that viruses use are molecules that are normally found on cell surfaces. Viruses have simply evolved to make use of these molecules for their own replication. For example,

HIV uses an adhesion molecule on T cells as one of its receptors. This adhesion molecule functions to keep different types of immune cells in close proximity to each other during an immune response.

Among the most complex virions known, the T4 bacteriophage, which infects the *Escherichia coli* bacterium, has a tail structure that the virus uses to attach to host cells and a head structure that houses its DNA.

Adenovirus, a non-enveloped animal virus that causes respiratory illnesses in humans, uses protein spikes protruding from its capsomeres to attach to host cells. Non-enveloped viruses also include those that cause polio (poliovirus), plantar warts (papillomavirus), and hepatitis A (hepatitis A virus).

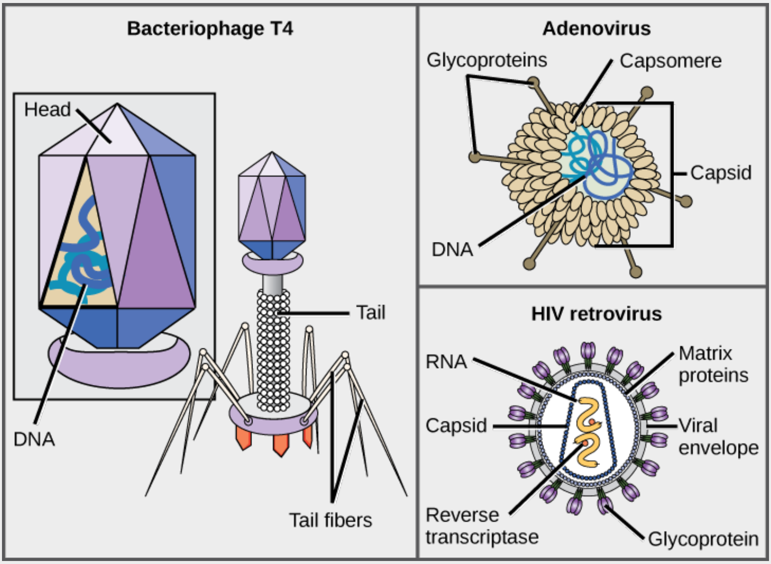
Enveloped virions like HIV, the causative agent in AIDS, consist of nucleic acid (RNA in the case of HIV) and capsid proteins surrounded by a lipid envelope and its associated proteins. Proteins embedded in the viral envelope are used to attach to host cells. Chicken pox, influenza, and mumps are examples of diseases caused by viruses with envelopes. Because of the fragility of the envelope, non-enveloped viruses are more resistant to changes in temperature, pH, and some disinfectants than enveloped viruses.

Overall, the shape of the virion and the presence or

absence of an envelope tell us little about what disease the virus may cause or what species it might infect, but they are still useful means to begin viral classification ([link]).

Art Connection

Viruses can be either complex in shape or relatively simple. This figure shows three relatively complex virions: the bacteriophage T4, with its DNA-containing head group and tail fibers that attach to host cells; adenovirus, which uses spikes from its capsid to bind to host cells; and HIV, which uses glycoproteins embedded in its envelope to bind to host cells. Notice that HIV has proteins called matrix proteins, internal to the envelope, which help stabilize virion shape. (credit "bacteriophage, adenovirus": modification of work by NCBI, NIH; credit "HIV retrovirus": modification of work by NIAID, NIH)



Which of the following statements about virus structure is true?

1. All viruses are encased in a viral membrane.
2. The capsomere is made up of small protein subunits called capsids.
3. DNA is the genetic material in all viruses.
4. Glycoproteins help the virus attach to the host cell.

Types of Nucleic Acid

Unlike nearly all living organisms that use DNA as their genetic material, viruses may use either DNA or RNA as theirs. The **virus core** contains the genome or total genetic content of the virus. Viral genomes tend to be small, containing only those

genes that encode proteins that the virus cannot get from the host cell. This genetic material may be single- or double-stranded. It may also be linear or circular. While most viruses contain a single nucleic acid, others have genomes that have several, which are called segments.

In DNA viruses, the viral DNA directs the host cell's replication proteins to synthesize new copies of the viral genome and to transcribe and translate that genome into viral proteins. DNA viruses cause human diseases, such as chickenpox, hepatitis B, and some venereal diseases, like herpes and genital warts.

RNA viruses contain only RNA as their genetic material. To replicate their genomes in the host cell, the RNA viruses encode enzymes that can replicate RNA into DNA, which cannot be done by the host cell. These RNA polymerase enzymes are more likely to make copying errors than DNA polymerases, and therefore often make mistakes during transcription. For this reason, mutations in RNA viruses occur more frequently than in DNA viruses. This causes them to change and adapt more rapidly to their host. Human diseases caused by RNA viruses include hepatitis C, measles, and rabies.

Steps of Viral Infection

The symptoms of viral diseases result from the immune response to the virus, which attempts to control and eliminate the virus from the body, and from cell damage caused by the virus. A virus must use cell processes to replicate. The viral replication cycle can produce dramatic changes in the host cell, which may cause cell damage. Some infected cells, such as those infected by the common cold virus known as rhinovirus, die through **lysis** (bursting) or apoptosis (programmed cell death or "cell suicide"), releasing all progeny virions at once. Many animal viruses, such as HIV (human immunodeficiency virus), leave the infected cells of the immune system by a process known as **budding**, where virions leave the cell individually. During the budding process, the cell is not immediately killed. However, the damage to the cell may make it impossible for the cells to function normally. Most productive viral infections follow similar steps in the virus replication cycle: attachment, penetration, uncoating, replication, assembly, and release ([link]).

Attachment

A virus attaches to a specific receptor site on the host cell membrane through attachment proteins in the capsid or via glycoproteins embedded in the viral envelope. The specificity of this interaction determines the host—and the cells within the host—that can be infected by a particular virus. This can

be illustrated by thinking of several keys and several locks, where each key will fit only one specific lock.

Link to Learning

This video explains how influenza attacks the body.

Entry

The nucleic acid of bacteriophages enters the host cell naked, leaving the capsid outside the cell. Plant and animal viruses can enter through endocytosis, in which the cell membrane surrounds and engulfs the entire virus. Some enveloped viruses enter the cell when the viral envelope fuses directly with the cell membrane. Once inside the cell, the viral capsid is degraded, and the viral nucleic acid is released, which then becomes available for replication and transcription.

Replication and Assembly

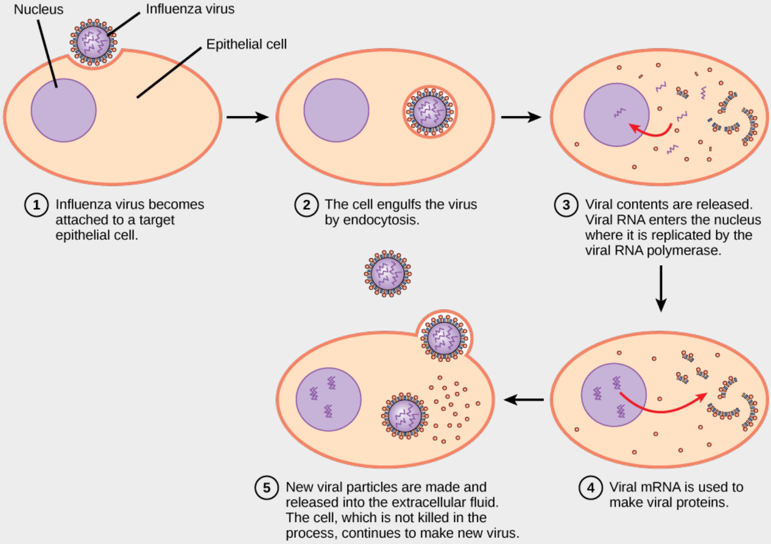
The replication mechanism depends on the viral genome. Some viruses come with their own DNA that is the blueprint for all the proteins that need to be made in the replication process. Other viruses use the host DNA to synthesize proteins. HIV for example produces some of its own enzymes not found in the host cell. This allowed researchers to develop drugs that inhibit these enzymes, targeting the virus specifically without affecting the host cell. This approach has led to the development of a variety of drugs used to treat HIV and has been effective at reducing the number of infectious virions (copies of viral RNA) in the blood to non-detectable levels in many HIV-infected individuals.

Release

The last stage of viral replication is the release of the new virions produced in the host organism, where they are able to infect adjacent cells and repeat the replication cycle. As you've learned, some viruses are released when the host cell dies, and other viruses can leave infected cells by budding through the membrane without directly killing the cell.

Art Connection

In influenza virus infection, glycoproteins attach to a host epithelial cell. As a result, the virus is engulfed. RNA and proteins are made and assembled into new virions.



Influenza virus is packaged in a viral envelope that fuses with the plasma membrane. This way, the virus can exit the host cell without killing it. What advantage does the virus gain by keeping the host cell alive?

Link to Learning

Click through a tutorial on viruses, identifying structures, modes of transmission, replication, and more.

Section Summary

Viruses are tiny, acellular entities that can usually only be seen with an electron microscope. Their genomes contain either DNA or RNA—never both—and they replicate using the replication proteins of a host cell. Viruses are diverse, infecting archaea, bacteria, fungi, plants, and animals. Viruses consist of a nucleic acid core surrounded by a protein capsid with or without an outer lipid envelope. The capsid shape, presence of an envelope, and core composition dictate some elements of the classification of viruses. Viral replication within a living cell always produces changes in the cell, sometimes resulting in cell death and sometimes slowly killing the infected cells. There are six basic stages in the virus replication cycle: attachment,

penetration, uncoating, replication, assembly, and release.

Art Connections

[link] Which of the following statements about virus structure is true?

1. All viruses are encased in a viral membrane.
2. The capsomere is made up of small protein subunits called capsids.
3. DNA is the genetic material in all viruses.
4. Glycoproteins help the virus attach to the host cell.

[link] D

[link] Influenza virus is packaged in a viral envelope that fuses with the plasma membrane. This way, the virus can exit the host cell without killing it. What advantage does the virus gain by keeping the host cell alive?

[link] The host cell can continue to make new virus particles.

Review Questions

Which statement is true?

1. A virion contains DNA and RNA.
2. Viruses are acellular.
3. Viruses replicate outside of the cell.
4. Most viruses are easily visualized with a light microscope.

B

The viral ______ plays a role in attaching a virion to the host cell.

1. core
2. capsid
3. envelope
4. both b and c

D

Viruses_____.

1. all have a round shape
2. cannot have a long shape
3. do not maintain any shape
4. vary in shape

D

Which statement is *not* true of viral replication?

1. Viruses won't always kill the host cell.
2. There are six basic steps in the viral replication cycle.
3. Viral replication does not affect host cell function.
4. Newly released virions can infect adjacent cells.

C

Which statement is true of viral replication?

1. In the process of apoptosis, the cell survives.
2. During attachment, the virus attaches at specific sites on the cell surface.
3. The viral capsid helps the host cell produce more copies of the viral genome.
4. mRNA works outside of the host cell to

produce enzymes and proteins.

B

Free Response

The first electron micrograph of a virus (tobacco mosaic virus) was produced in 1939. Before that time, how did scientists know that viruses existed if they could not see them? (Hint: Early scientists called viruses “filterable agents.”)

Viruses pass through filters that eliminated all bacteria that were visible in the light microscopes at the time. As the bacteria-free filtrate could still cause infections when given to a healthy organism, this observation demonstrated the existence of very small infectious agents. These agents were later shown to be unrelated to bacteria and were classified as viruses.

Glossary

acellular
: lacking cells

budding
: method of exit from the cell used in certain animal viruses, where virions leave the cell individually by capturing a piece of the host plasma membrane

capsid
: protein coating of the viral core

capsomere
: protein subunit that makes up the capsid

envelope
: lipid bilayer that envelopes some viruses

lysis
: bursting of a cell

viral receptor
: glycoprotein used to attach a virus to host cells via molecules on the cell

virion
: individual virus particle outside a host cell

virus core
: contains the virus genome

Bacteria and Archaea
By the end of this section, you will be able to:

- Describe the evolutionary history of prokaryotes
- Describe the basic structure of a typical prokaryote
- Identify bacterial diseases that caused historically important plagues and epidemics
- Describe the uses of prokaryotes in food processing and bioremediation

Certain prokaryotes can live in extreme environments such as the Morning Glory pool, a hot spring in Yellowstone National Park. The spring's vivid blue color is from the prokaryotes that thrive in its very hot waters. (credit: modification of work by Jon Sullivan)

Introduction

In the recent past, scientists grouped living things into five kingdoms—animals, plants, fungi, protists, and prokaryotes—based on several criteria, such as the absence or presence of a nucleus and other membrane-bound organelles, the absence or presence of cell walls, multicellularity, and so on. In the late 20th century, the pioneering work of Carl Woese and others compared sequences of small-subunit ribosomal RNA (SSU rRNA), which resulted in a more fundamental way to group organisms on Earth. Based on differences in the structure of cell membranes and in rRNA, Woese and his colleagues proposed that all life on Earth evolved along three lineages, called domains. The domain Bacteria comprises all organisms in the kingdom Bacteria, the domain Archaea comprises the rest of the prokaryotes, and the domain Eukarya comprises all eukaryotes—including organisms in the kingdoms Animalia, Plantae, Fungi, and Protista.

Two of the three domains—Bacteria and Archaea—are prokaryotic. Prokaryotes were the first inhabitants on Earth, appearing 3.5 to 3.8 billion years ago. These organisms are abundant and ubiquitous; that is, they are present everywhere. In addition to inhabiting moderate environments, they are found in extreme conditions: from boiling springs to permanently frozen environments in Antarctica; from salty environments like the Dead Sea to environments under tremendous pressure, such as the depths of the ocean; and from areas without oxygen, such as a waste management plant, to radioactively contaminated regions, such as Chernobyl. Prokaryotes reside in the human digestive system and on the skin, are responsible for certain illnesses, and serve an important role in the preparation of many foods.

Prokaryotes are present everywhere. They cover every imaginable surface where there is sufficient moisture, and they live on and inside of other living things. There are more prokaryotes inside and on the exterior of the human body than there are human cells in the body. Some prokaryotes thrive in environments that are inhospitable for most other living things. Prokaryotes recycle **nutrients**—essential substances (such as carbon and nitrogen)—and they drive the evolution of new ecosystems, some of which are natural while others are man-made. Prokaryotes have been on Earth since long before multicellular life appeared.

Prokaryotic Diversity

The advent of DNA sequencing provided immense insight into the relationships and origins of prokaryotes that were not possible using traditional methods of classification. A major insight identified two groups of prokaryotes that were found to be as different from each other as they were from eukaryotes. This recognition of prokaryotic diversity forced a new understanding of the classification of all life and brought us closer to understanding the fundamental relationships of all living things, including ourselves.

Biofilms

Until a couple of decades ago, microbiologists thought of prokaryotes as isolated entities living apart. This model, however, does not reflect the true ecology of prokaryotes, most of which prefer to live in communities where they can interact. A **biofilm** is a microbial community held together in a gummy-textured matrix, consisting primarily of polysaccharides secreted by the organisms, together with some proteins and nucleic acids. Biofilms grow attached to surfaces. Some of the best-studied biofilms are composed of prokaryotes, although

fungal biofilms have also been described.

Biofilms are present almost everywhere. They cause the clogging of pipes and readily colonize surfaces in industrial settings. They have played roles in recent, large-scale outbreaks of bacterial contamination of food. Biofilms also colonize household surfaces, such as kitchen counters, cutting boards, sinks, and toilets.

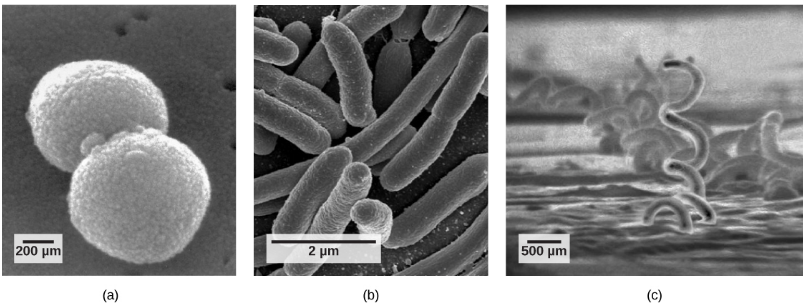
Interactions among the organisms that populate a biofilm, together with their protective environment, make these communities more robust than are free-living, or planktonic, prokaryotes. The sticky substance that holds bacteria together also excludes most antibiotics and disinfectants, making biofilm bacteria hardier than their planktonic counterparts. Overall, biofilms are very difficult to destroy, because they are resistant to many of the common forms of sterilization.

Many prokaryotes fall into three basic categories based on their shape: (a) cocci, or spherical; (b) bacilli, or rod-shaped; and (c) spirilla, or spiral-shaped. (credit a: modification of work by Janice Haney Carr, Dr. Richard Facklam, CDC; credit c: modification of work by Dr. David Cox, CDC; scale-bar data from Matt Russell)

Characteristics of Prokaryotes

There are many differences between prokaryotic and

eukaryotic cells. However, all cells have four common structures: a plasma membrane that functions as a barrier for the cell and separates the cell from its environment; cytoplasm, a jelly-like substance inside the cell; genetic material (DNA and RNA); and ribosomes, where protein synthesis takes place. Prokaryotes come in various shapes, but many fall into three categories: cocci (spherical), bacilli (rod-shaped), and spirilla (spiral-shaped) ([link]).

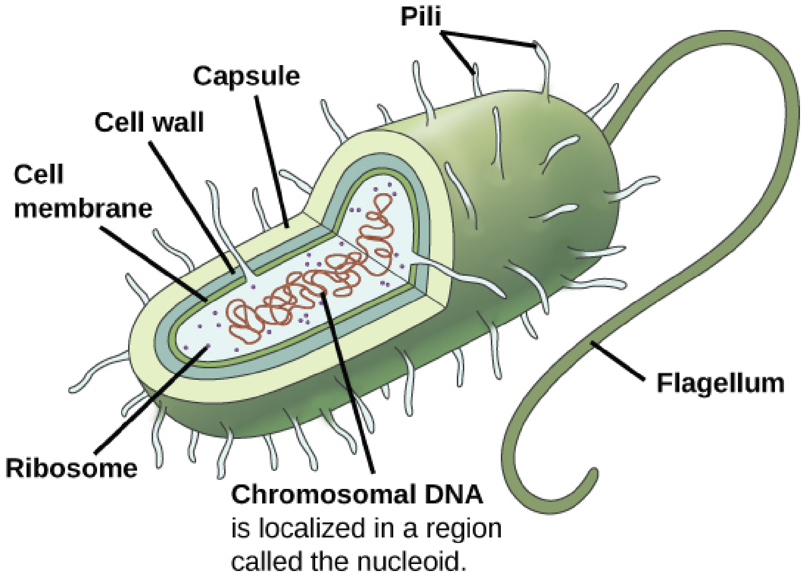


The features of a typical bacterium cell are shown.

The Prokaryotic Cell

Recall that prokaryotes ([link]) are unicellular organisms that lack organelles surrounded by membranes. Therefore, they do not have a nucleus but instead have a single chromosome—a piece of circular DNA located in an area of the cell called the nucleoid. Most prokaryotes have a cell wall lying outside the plasma membrane. The composition of the cell wall differs significantly between the domains Bacteria and Archaea (and their cell walls also differ from the eukaryotic cell walls found in

plants and fungi.) The cell wall functions as a protective layer and is responsible for the organism's shape. Some other structures are present in some prokaryotic species, but not in others. For example, the **capsule** found in some species enables the organism to attach to surfaces and protects it from dehydration. Some species may also have flagella (singular, flagellum) used for locomotion, and pili (singular, pilus) used for attachment to surfaces and to other bacteria for conjugation. Plasmids, which consist of small, circular pieces of DNA outside of the main chromosome, are also present in many species of bacteria.



Both Bacteria and Archaea are types of prokaryotic cells. They differ in the lipid composition of their cell membranes and in the characteristics of their cell walls. Both types of prokaryotes have the same

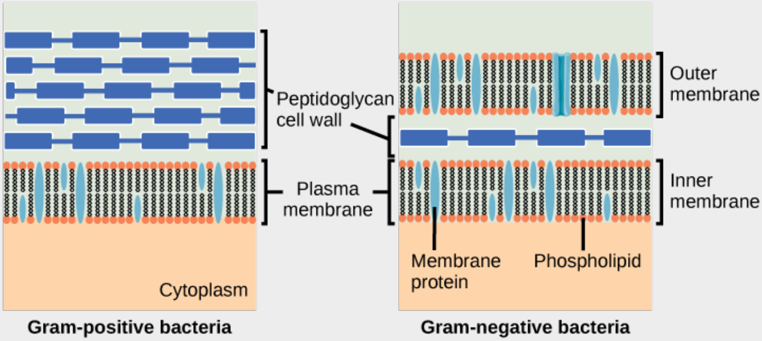
basic structures, but these are built from different chemical components that are evidence of an ancient separation of their lineages. The archaeal plasma membrane is chemically different from the bacterial membrane; some archaeal membranes are lipid monolayers instead of phosopholipid bilayers.

The Cell Wall

The cell wall is a protective layer that surrounds some prokaryotic cells and gives them shape and rigidity. It is located outside the cell membrane and prevents osmotic lysis (bursting caused by increasing volume). The chemical compositions of the cell walls vary between Archaea and Bacteria, as well as between bacterial species. Bacterial cell walls contain **peptidoglycan**, composed of polysaccharide chains cross-linked to peptides. Bacteria are divided into two major groups: **Gram-positive** and **Gram-negative**, based on their reaction to a procedure called Gram staining. The different bacterial responses to the staining procedure are caused by cell wall structure. Gram-positive organisms have a thick wall consisting of many layers of peptidoglycan. Gram-negative bacteria have a thinner cell wall composed of a few layers of peptidoglycan and additional structures, surrounded by an outer membrane ([link]).

Art Connection

Bacteria are divided into two major groups: Gram-positive and Gram-negative. Both groups have a cell wall composed of peptidoglycans: In Gram-positive bacteria, the wall is thick, whereas in Gram-negative bacteria, the wall is thin. In Gram-negative bacteria, the cell wall is surrounded by an outer membrane.



Which of the following statements is true?

1. Gram-positive bacteria have a single cell wall formed from peptidoglycan.
2. Gram-positive bacteria have an outer membrane.
3. The cell wall of Gram-negative bacteria is thick, and the cell wall of Gram-positive bacteria is thin.
4. Gram-negative bacteria have a cell wall made of peptidoglycan, while Gram-positive bacteria have a cell wall made of phospholipids.

Archaeal cell walls do not contain peptidoglycan.

There are four different types of archaeal cell walls. One type is composed of **pseudopeptidoglycan**. The other three types of cell walls contain polysaccharides, glycoproteins, and surface-layer proteins known as S-layers.

Reproduction

Reproduction in prokaryotes is primarily asexual and takes place by binary fission. Recall that the DNA of a prokaryote exists usually as a single, circular chromosome. Prokaryotes do not undergo mitosis. Rather, the chromosome loop is replicated, and the two resulting copies attached to the plasma membrane move apart as the cell grows in a process called binary fission. The prokaryote, now enlarged, is pinched inward at its equator, and the two resulting cells, which are clones, separate. Binary fission does not provide an opportunity for genetic recombination, but prokaryotes can alter their genetic makeup in three ways.

In a process called **transformation**, the cell takes in DNA found in its environment that is shed by other prokaryotes, alive or dead. A **pathogen** is an organism that causes a disease. If a nonpathogenic bacterium takes up DNA from a pathogen and incorporates the new DNA in its own chromosome, it too may become pathogenic. In **transduction**, bacteriophages, the viruses that infect bacteria,

move DNA from one bacterium to another. Archaea have a different set of viruses that infect them and translocate genetic material from one individual to another. During **conjugation**, DNA is transferred from one prokaryote to another by means of a pilus that brings the organisms into contact with one another. The DNA transferred is usually a plasmid, but parts of the chromosome can also be moved.

Cycles of binary fission can be very rapid, on the order of minutes for some species. This short generation time coupled with mechanisms of genetic recombination result in the rapid evolution of prokaryotes, allowing them to respond to environmental changes (such as the introduction of an antibiotic) very quickly.

How Prokaryotes Obtain Energy and Carbon

Prokaryotes are metabolically diverse organisms. Prokaryotes fill many niches on Earth, including being involved in nutrient cycles such as the nitrogen and carbon cycles, decomposing dead organisms, and growing and multiplying inside living organisms, including humans. Different prokaryotes can use different sources of energy to assemble macromolecules from smaller molecules. Phototrophs obtain their energy from sunlight. Chemotrophs obtain their energy from chemical compounds.

Bacterial Diseases in Humans

Devastating pathogen-borne diseases and plagues, both viral and bacterial in nature, have affected and continue to affect humans. It is worth noting that all pathogenic prokaryotes are Bacteria; there are no known pathogenic Archaea in humans or any other organism. Pathogenic organisms evolved alongside humans. In the past, the true cause of these diseases was not understood, and some cultures thought that diseases were a spiritual punishment or were mistaken about material causes. Over time, people came to realize that staying apart from afflicted persons, improving sanitation, and properly disposing of the corpses and personal belongings of victims of illness reduced their own chances of getting sick.

Papagrigorakis M. J., Synodinos P. N., Yapijakis C, "Ancient typhoid epidemic reveals possible ancestral strain of *Salmonella enterica* serovar Typhi, *Infect Genet Evol* 7 (2007): 126-7.

Historical Perspective

There are records of infectious diseases as far back as 3,000 B.C. A number of significant **pandemics** caused by Bacteria have been documented over several hundred years. Some of the largest pandemics led to the decline of cities and cultures. Many were zoonoses that appeared with the domestication of animals, as in the case of

tuberculosis. A zoonosis is a disease that infects animals but can be transmitted from animals to humans.

Infectious diseases remain among the leading causes of death worldwide. Their impact is less significant in many developed countries, but they are important determiners of mortality in developing countries. The development of antibiotics did much to lessen the mortality rates from bacterial infections, but access to antibiotics is not universal, and the overuse of antibiotics has led to the development of resistant strains of bacteria. Public sanitation efforts that dispose of sewage and provide clean drinking water have done as much or more than medical advances to prevent deaths caused by bacterial infections.

In 430 B.C., the plague of Athens killed one-quarter of the Athenian troops that were fighting in the Great Peloponnesian War. The disease killed a quarter of the population of Athens in over 4 years and weakened Athens' dominance and power. The source of the plague may have been identified recently when researchers from the University of Athens were able to analyze DNA from teeth recovered from a mass grave. The scientists identified nucleotide sequences from a pathogenic bacterium that causes typhoid fever.[footnote]

From 541 to 750 A.D., an outbreak called the plague

of Justinian (likely a bubonic plague) eliminated, by some estimates, one-quarter to one-half of the human population. The population in Europe declined by 50 percent during this outbreak. Bubonic plague would decimate Europe more than once.

One of the most devastating pandemics was the **Black Death** (1346 to 1361), which is believed to have been another outbreak of bubonic plague caused by the bacterium *Yersinia pestis*. This bacterium is carried by fleas living on black rats. The Black Death reduced the world's population from an estimated 450 million to about 350 to 375 million. Bubonic plague struck London hard again in the mid-1600s. There are still approximately 1,000 to 3,000 cases of plague globally each year. Although contracting bubonic plague before antibiotics meant almost certain death, the bacterium responds to several types of modern antibiotics, and mortality rates from plague are now very low.

Concept in Action

Watch a video on the modern understanding of the Black Death (bubonic plague) in Europe during the fourteenth century.

Over the centuries, Europeans developed resistance to many infectious diseases. However, European conquerors brought disease-causing bacteria and viruses with them when they reached the Western hemisphere, triggering **epidemics** that completely devastated populations of Native Americans (who had no natural resistance to many European diseases).

Naimi, T. S., LeDell, K. H., Como-Sabetti, K., et al., "Comparison of community- and health care-associated methicillin-resistant *Staphylococcus aureus* infection," *JAMA* 290 (2003): 2976-2984, doi: 10.1001/jama.290.22.2976.This scanning electron micrograph shows methicillin-resistant *Staphylococcus aureus* bacteria, commonly known as MRSA. (credit: modification of work by Janice Haney Carr, CDC; scale-bar data from Matt Russell)

The Antibiotic Crisis

The word antibiotic comes from the Greek *anti*, meaning “against,” and *bios*, meaning “life.” An antibiotic is an organism-produced chemical that is hostile to the growth of other organisms. Today’s news and media often address concerns about an antibiotic crisis. Are antibiotics that were used to treat bacterial infections easily treatable in the past becoming obsolete? Are there new “superbugs”—bacteria that have evolved to become more resistant to our arsenal of antibiotics? Is this the beginning of the end of antibiotics? All of these questions challenge the healthcare community.

One of the main reasons for resistant bacteria is the overuse and incorrect use of antibiotics, such as not completing a full course of prescribed antibiotics. The incorrect use of an antibiotic results in the natural selection of resistant forms of bacteria. The antibiotic kills most of the infecting bacteria, and therefore only the resistant forms remain. These resistant forms reproduce, resulting in an increase in the proportion of resistant forms over non-resistant ones.

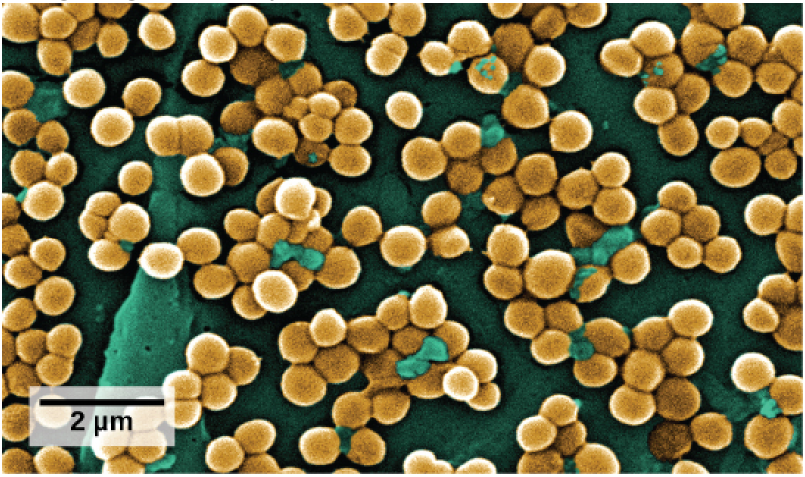
Another problem is the excessive use of antibiotics in livestock. The routine use of antibiotics in animal feed promotes bacterial resistance as well. In the United States, 70 percent of the antibiotics produced are fed to animals. The antibiotics are not used to prevent disease, but to enhance production of their products.

Concept in Action

Watch a recent news report on the problem of routine antibiotic administration to livestock and antibiotic-resistant bacteria.

Staphylococcus aureus, often called “staph,” is a common bacterium that can live in and on the human body, which usually is easily treatable with antibiotics. A very dangerous strain, however, has made the news over the past few years ([link]). This strain, **methicillin-resistant *Staphylococcus aureus* (MRSA)**, is resistant to many commonly used antibiotics, including methicillin, amoxicillin, penicillin, and oxacillin. While MRSA infections have been common among people in healthcare facilities, it is appearing more commonly in healthy people who live or work in dense groups (like military personnel and prisoners). The *Journal of the American Medical Association* reported that, among MRSA-afflicted persons in healthcare facilities, the average age is 68 years, while people with

“community-associated MRSA” (CA-MRSA) have an average age of 23 years.[footnote]



In summary, society is facing an antibiotic crisis. Some scientists believe that after years of being protected from bacterial infections by antibiotics, we may be returning to a time in which a simple bacterial infection could again devastate the human population. Researchers are working on developing new antibiotics, but few are in the drug development pipeline, and it takes many years to generate an effective and approved drug.

http://www.cdc.gov/ecoli/2006/september, Centers for Disease Control and Prevention, “Multi-state outbreak of *E. coli* O157:H7 infections from spinach,” September-October (2006).(a) Locally grown vegetable sprouts were the cause of a European *E. coli* outbreak that killed 31 people and sickened about 3,000 in 2010. (b) *Escherichia coli* are shown here in a scanning electron micrograph. The strain of *E. coli* that caused a deadly outbreak in

Germany is a new one not involved in any previous *E. coli* outbreaks. It has acquired several antibiotic resistance genes and specific genetic sequences involved in aggregation ability and virulence. It has recently been sequenced. (credit b: Rocky Mountain Laboratories, NIAID, NIH; scale-bar data from Matt Russell)

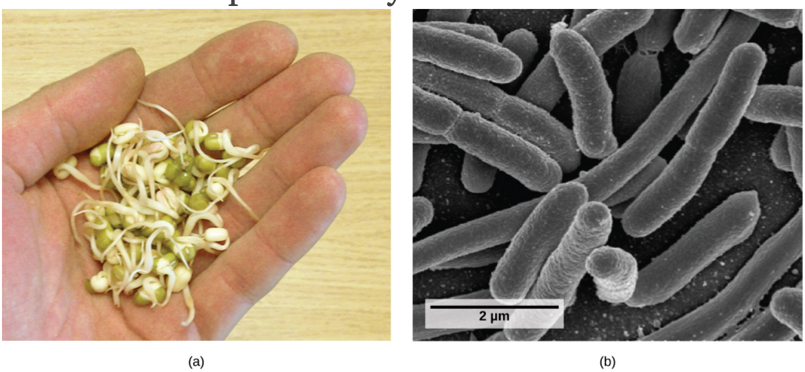
Foodborne Diseases

Prokaryotes are everywhere: They readily colonize the surface of any type of material, and food is not an exception. Outbreaks of bacterial infection related to food consumption are common. A **foodborne disease** (colloquially called "food poisoning") is an illness resulting from the consumption of food contaminated with pathogenic bacteria, viruses, or other parasites. Although the United States has one of the safest food supplies in the world, the Center for Disease Control and Prevention (CDC) has reported that "76 million people get sick, more than 300,000 are hospitalized, and 5,000 Americans die each year from foodborne illness."[footnote]

The characteristics of foodborne illnesses have changed over time. In the past, it was relatively common to hear about sporadic cases of **botulism**, the potentially fatal disease produced by a toxin from the anaerobic bacterium *Clostridium botulinum*. A can, jar, or package created a suitable anaerobic

environment where *Clostridium* could grow. Proper sterilization and canning procedures have reduced the incidence of this disease.

Most cases of foodborne illnesses are now linked to produce contaminated by animal waste. For example, there have been serious, produce-related outbreaks associated with raw spinach in the United States and with vegetable sprouts in Germany ([link]). The raw spinach outbreak in 2006 was produced by the bacterium *E. coli* strain O157:H7. Most *E. coli* strains are not particularly dangerous to humans, (indeed, they live in our large intestine), but O157:H7 is potentially fatal.



All types of food can potentially be contaminated with harmful bacteria of different species. Recent outbreaks of *Salmonella* reported by the CDC occurred in foods as diverse as peanut butter, alfalfa sprouts, and eggs.

Careers in Action

Epidemiologist

Epidemiology is the study of the occurrence, distribution, and determinants of health and disease in a population. It is, therefore, related to public health. An epidemiologist studies the frequency and distribution of diseases within human populations and environments.

Epidemiologists collect data about a particular disease and track its spread to identify the original mode of transmission. They sometimes work in close collaboration with historians to try to understand the way a disease evolved geographically and over time, tracking the natural history of pathogens. They gather information from clinical records, patient interviews, and any other available means. That information is used to develop strategies and design public health policies to reduce the incidence of a disease or to prevent its spread. Epidemiologists also conduct rapid investigations in case of an outbreak to recommend immediate measures to control it.

Epidemiologists typically have a graduate-level education. An epidemiologist often has a bachelor’s degree in some field and a master’s degree in public health (MPH). Many epidemiologists are also physicians (and have an MD) or they have a PhD in an associated field, such as biology or epidemiology.

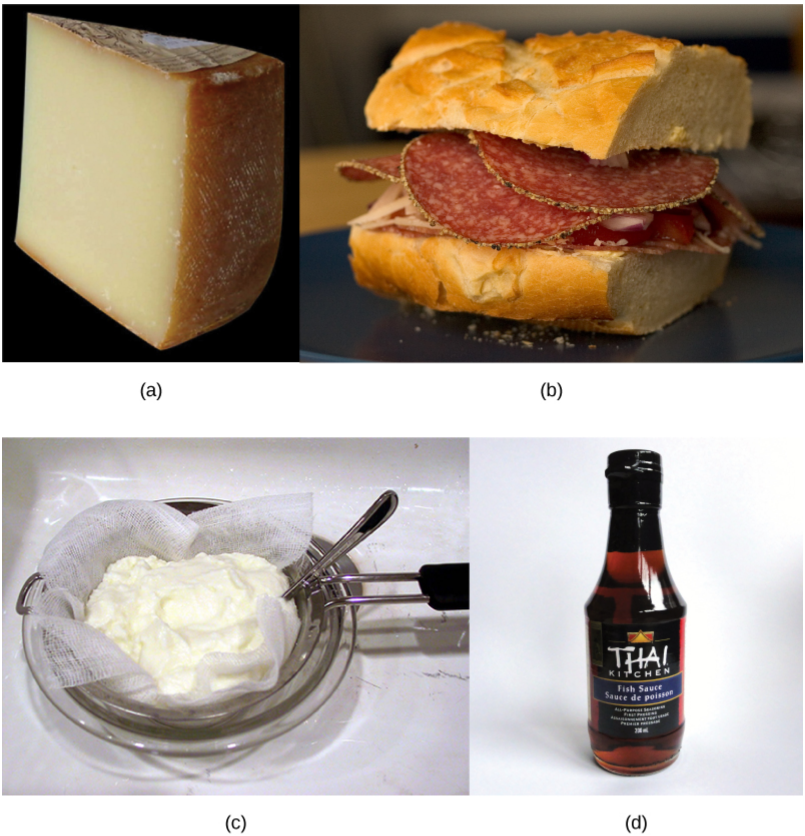
Beneficial Prokaryotes

Not all prokaryotes are pathogenic. On the contrary, pathogens represent only a very small percentage of the diversity of the microbial world. In fact, our life and all life on this planet would not be possible without prokaryotes.
http://www.cbd.int/convention/articles/?a=cbd-02http://www.cbd.int/convention/articles/?a=cbd-02, United Nations Convention on Biological Diversity, “Article 2: Use of Terms.”Some of the products derived from the use of prokaryotes in early biotechnology include (a) cheese, (b) salami, (c) yogurt, and (d) fish sauce. (credit b: modification of work by Alisdair McDiarmid; credit c: modification of work by Kris Miller; credit d: modification of work by Jane Whitney)

Prokaryotes, and Food and Beverages

According to the United Nations Convention on Biological Diversity, biotechnology is “any technological application that uses biological systems, living organisms, or derivatives thereof, to make or modify products or processes for specific use.”[footnote] The concept of “specific use” involves some sort of commercial application. Genetic engineering, artificial selection, antibiotic

production, and cell culture are current topics of study in biotechnology. However, humans have used prokaryotes to create products before the term biotechnology was even coined. And some of the goods and services are as simple as cheese, yogurt, sour cream, vinegar, cured sausage, sauerkraut, and fermented seafood that contains both bacteria and archaea ([link]).



Cheese production began around 4,000 years ago when humans started to breed animals and process their milk. Evidence suggests that cultured milk products, like yogurt, have existed for at least 4,000

years.

(a) Cleaning up oil after the Valdez spill in Alaska, the workers hosed oil from beaches and then used a floating boom to corral the oil, which was finally skimmed from the water surface. Some species of bacteria are able to solubilize and degrade the oil. (b) One of the most catastrophic consequences of oil spills is the damage to fauna. (credit a: modification of work by NOAA; credit b: modification of work by GOLUBENKOV, NGO: Saving Taman)

Using Prokaryotes to Clean up Our Planet: Bioremediation

Microbial **bioremediation** is the use of prokaryotes (or microbial metabolism) to remove pollutants. Bioremediation has been used to remove agricultural chemicals (pesticides and fertilizers) that leach from soil into groundwater. Certain toxic metals, such as selenium and arsenic compounds, can also be removed from water by bioremediation. The reduction of SeO_4^{2-} to SeO_3^{2-} and to Se^0 (metallic selenium) is a method used to remove selenium ions from water. Mercury is an example of a toxic metal that can be removed from an environment by bioremediation. Mercury is an active ingredient of some pesticides; it is used in industry and is also a byproduct of certain industries, such as battery production. Mercury is usually present in very low concentrations in natural environments but it is highly toxic because

it accumulates in living tissues. Several species of bacteria can carry out the biotransformation of toxic mercury into nontoxic forms. These bacteria, such as *Pseudomonas aeruginosa*, can convert Hg^{2+} to Hg^{0}, which is nontoxic to humans.

Probably one of the most useful and interesting examples of the use of prokaryotes for bioremediation purposes is the cleanup of oil spills. The importance of prokaryotes to petroleum bioremediation has been demonstrated in several oil spills in recent years, such as the Exxon Valdez spill in Alaska (1989) ([link]), the Prestige oil spill in Spain (2002), the spill into the Mediterranean from a Lebanon power plant (2006,) and more recently, the BP oil spill in the Gulf of Mexico (2010). To clean up these spills, bioremediation is promoted by adding inorganic nutrients that help bacteria already present in the environment to grow. Hydrocarbon-degrading bacteria feed on the hydrocarbons in the oil droplet, breaking them into inorganic compounds. Some species, such as *Alcanivorax borkumensis*, produce surfactants that solubilize the oil, while other bacteria degrade the oil into carbon dioxide. In the case of oil spills in the ocean, ongoing, natural bioremediation tends to occur, inasmuch as there are oil-consuming bacteria in the ocean prior to the spill. Under ideal conditions, it has been reported that up to 80 percent of the nonvolatile components in oil can be degraded within 1 year of the spill. Other oil

fractions containing aromatic and highly branched hydrocarbon chains are more difficult to remove and remain in the environment for longer periods of time. Researchers have genetically engineered other bacteria to consume petroleum products; indeed, the first patent application for a bioremediation application in the U.S. was for a genetically modified oil-eating bacterium.

(a) (b)

Prokaryotes in and on the Body

Humans are no exception when it comes to forming symbiotic relationships with prokaryotes. We are accustomed to thinking of ourselves as single organisms, but in reality, we are walking ecosystems. There are 10 to 100 times as many bacterial and archaeal cells inhabiting our bodies as we have cells in our bodies. Some of these are in mutually beneficial relationships with us, in which both the human host and the bacterium benefit, while some of the relationships are classified as **commensalism**, a type of relationship in which the bacterium benefits and the human host is neither benefited nor harmed.

Human gut flora lives in the large intestine and consists of hundreds of species of bacteria and archaea, with different individuals containing different species mixes. The term “flora,” which is usually associated with plants, is traditionally used in this context because bacteria were once classified as plants. The primary functions of these prokaryotes for humans appear to be metabolism of food molecules that we cannot break down, assistance with the absorption of ions by the colon, synthesis of vitamin K, training of the infant immune system, maintenance of the adult immune system, maintenance of the epithelium of the large intestine, and formation of a protective barrier against pathogens.

The surface of the skin is also coated with prokaryotes. The different surfaces of the skin, such as the underarms, the head, and the hands, provide different habitats for different communities of prokaryotes. Unlike with gut flora, the possible beneficial roles of skin flora have not been well studied. However, the few studies conducted so far have identified bacteria that produce antimicrobial compounds as probably responsible for preventing infections by pathogenic bacteria.

Researchers are actively studying the relationships between various diseases and alterations to the composition of human microbial flora. Some of this work is being carried out by the Human Microbiome

Project, funded in the United States by the National Institutes of Health.

Section Summary

Prokaryotes existed for billions of years before plants and animals appeared. Microbial mats are thought to represent the earliest forms of life on Earth, and there is fossil evidence, called stromatolites, of their presence about 3.5 billion years ago. During the first 2 billion years, the atmosphere was anoxic and only anaerobic organisms were able to live. Cyanobacteria began the oxygenation of the atmosphere. The increase in oxygen concentration allowed the evolution of other life forms.

Prokaryotes (domains Archaea and Bacteria) are single-celled organisms lacking a nucleus. They have a single piece of circular DNA in the nucleoid area of the cell. Most prokaryotes have cell wall outside the plasma membrane. Bacteria and Archaea differ in the compositions of their cell membranes and the characteristics of their cell walls.

Bacterial cell walls contain peptidoglycan. Archaean cell walls do not have peptidoglycan. Bacteria can be divided into two major groups: Gram-positive and Gram-negative. Gram-positive organisms have a thick cell wall. Gram-negative organisms have a thin

cell wall and an outer membrane. Prokaryotes use diverse sources of energy to assemble macromolecules from smaller molecules. Phototrophs obtain their energy from sunlight, whereas chemotrophs obtain it from chemical compounds.

Infectious diseases caused by bacteria remain among the leading causes of death worldwide. The excessive use of antibiotics to control bacterial infections has resulted in resistant forms of bacteria being selected. Foodborne diseases result from the consumption of contaminated food, pathogenic bacteria, viruses, or parasites that contaminate food. Prokaryotes are used in human food products. Microbial bioremediation is the use of microbial metabolism to remove pollutants. The human body contains a huge community of prokaryotes, many of which provide beneficial services such as the development and maintenance of the immune system, nutrition, and protection from pathogens.

Art Connections

[link] Which of the following statements is true?

1. Gram-positive bacteria have a single cell

wall formed from peptidoglycan.
2. Gram-positive bacteria have an outer membrane.
3. The cell wall of Gram-negative bacteria is thick, and the cell wall of Gram-positive bacteria is thin.
4. Gram-negative bacteria have a cell wall made of peptidoglycan, while Gram-positive bacteria have a cell wall made of phospholipids.

[link] A

Multiple Choice

The first forms of life on Earth were thought to be_____.

1. single-celled plants
2. prokaryotes
3. insects
4. large animals such as dinosaurs

B

The first organisms that oxygenated the atmosphere were _____.

1. cyanobacteria
2. phototrophic organisms
3. anaerobic organisms
4. all of the above

A

Which of the following consist of prokaryotic cells?

1. bacteria and fungi
2. archaea and fungi
3. protists and animals
4. bacteria and archaea

D

Prokaryotes stain as Gram-positive or Gram-negative because of differences in the _____.

1. cell wall
2. cytoplasm
3. nucleus
4. chromosome

A

Prokaryotes that obtain their energy from chemical compounds are called ____.

1. phototrophs
2. auxotrophs
3. chemotrophs
4. lithotrophs

C

Bioremediation includes ____.

1. the use of prokaryotes that can fix nitrogen
2. the use of prokaryotes to clean up pollutants
3. the use of prokaryotes as natural fertilizers
4. All of the above

B

Free Response

Explain the reason why the imprudent and

excessive use of antibiotics has resulted in a major global problem.

Antibiotics kill bacteria that are sensitive to them; thus, only the resistant ones will survive. These resistant bacteria will reproduce, and therefore, after a while, there will be only resistant bacteria, making it more difficult to treat the diseases they may cause in humans.

Your friend believes that prokaryotes are always detrimental and pathogenic. How would you explain to them that they are wrong?

Remind them of the important roles prokaryotes play in decomposition and freeing up nutrients in biogeochemical cycles; remind them of the many prokaryotes that are not human pathogens and that fill very specialized niches.

Glossary

anaerobic
: refers to organisms that grow without oxygen

anoxic
: without oxygen

biofilm

a microbial community that is held together by a gummy-textured matrix

bioremediation

the use of microbial metabolism to remove pollutants

Black Death

a devastating pandemic that is believed to have been an outbreak of bubonic plague caused by the bacterium *Yersinia pestis*

botulism

a disease produce by the toxin of the anaerobic bacterium *Clostridium botulinum*

capsule

an external structure that enables a prokaryote to attach to surfaces and protects it from dehydration

commensalism

a symbiotic relationship in which one member benefits while the other member is not affected

conjugation

the process by which prokaryotes move DNA from one individual to another using a pilus

cyanobacteria

bacteria that evolved from early phototrophs and oxygenated the atmosphere; also known as blue-green algae

epidemic
: a disease that occurs in an unusually high number of individuals in a population at the same time

extremophile
: an organism that grows under extreme or harsh conditions

foodborne disease
: any illness resulting from the consumption of contaminated food, or of the pathogenic bacteria, viruses, or other parasites that contaminate food

Gram-negative
: describes a bacterium whose cell wall contains little peptidoglycan but has an outer membrane

Gram-positive
: describes a bacterium that contains mainly peptidoglycan in its cell walls

hydrothermal vent
: a fissure in Earth’s surface that releases geothermally heated water

microbial mat
: a multi-layered sheet of prokaryotes that may include bacteria and archaea

MRSA
: (methicillin-resistant *Staphylococcus aureus*) a very dangerous *Staphylococcus aureus* strain resistant to antibiotics

pandemic
: a widespread, usually worldwide, epidemic disease

pathogen
: an organism, or infectious agent, that causes a disease

peptidoglycan
: a material composed of polysaccharide chains cross-linked to unusual peptides

phototroph
: an organism that uses energy from sunlight

pseudopeptidoglycan
: a component of some cell walls of Archaea

stromatolite
: a layered sedimentary structure formed by precipitation of minerals by prokaryotes in microbial mats

transduction

the process by which a bacteriophage moves DNA from one prokaryote to another

transformation
: a mechanism of genetic change in prokaryotes in which DNA present in the environment is taken into the cell and incorporated into the genome

Prions and Viroids
By the end of this section, you will be able to do the following:

- Describe prions and their basic properties
- Define viroids and their targets of infection

Prions and viroids are **pathogens** (agents with the ability to cause disease) that have simpler structures than viruses but, in the case of prions, still can produce deadly diseases.
Mad Cow Disease in humans. (a) Endogenous normal prion protein (PrP_c) is converted into the disease-causing form (PrP_{sc}) when it encounters this variant form of the protein. PrP_{sc} may arise spontaneously in brain tissue, especially if a mutant form of the protein is present, or it may occur via the spread of misfolded prions consumed in food into brain tissue. (b) This prion-infected brain tissue, visualized using light microscopy, shows the vacuoles that give it a spongy texture, typical of transmissible spongiform encephalopathies. (credit b: modification of work by Dr. Al Jenny, USDA APHIS; scale-bar data from Matt Russell)

Prions

Prions, so-called because they are proteinaceous, are infectious particles—smaller than viruses—that contain no nucleic acids (neither DNA nor RNA).

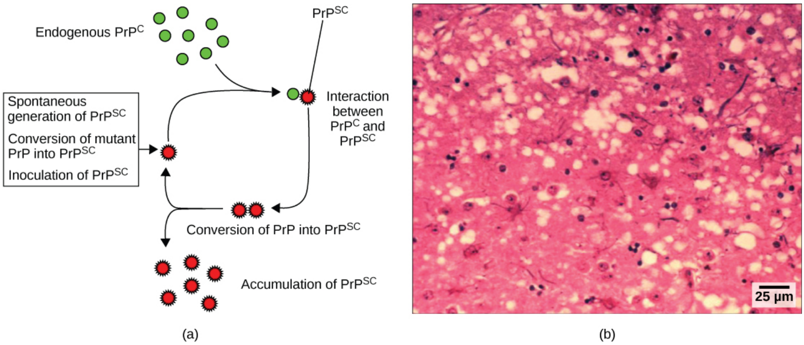
Historically, the idea of an infectious agent that did not use nucleic acids was considered impossible, but pioneering work by Nobel Prize-winning biologist Stanley Prusiner has convinced the majority of biologists that such agents do indeed exist.

Fatal neurodegenerative diseases, such as kuru in humans and bovine spongiform encephalopathy (BSE) in cattle (commonly known as “mad cow disease”) were shown to be transmitted by prions. The disease was spread by the consumption of meat, nervous tissue, or internal organs between members of the same species. Kuru, native to humans in Papua New Guinea, was spread from human to human via ritualistic cannibalism. BSE, originally detected in the United Kingdom, was spread between cattle by the practice of including cattle nervous tissue in feed for other cattle. Individuals with kuru and BSE show symptoms of loss of motor control and unusual behaviors, such as uncontrolled bursts of laughter with kuru, followed by death. Kuru was controlled by inducing the population to abandon its ritualistic cannibalism.

On the other hand, BSE was initially thought to only affect cattle. Cattle dying of the disease were shown to have developed lesions or “holes” in the brain, causing the brain tissue to resemble a sponge. Later on in the outbreak, however, it was shown that a similar encephalopathy in humans, known as variant Creutzfeldt-Jakob disease (CJD), could be

acquired from eating beef from animals infected with BSE, sparking bans by various countries on the importation of British beef and causing considerable economic damage to the British beef industry ([link]). BSE still exists in various areas, and although a rare disease, individuals that acquire CJD are difficult to treat. The disease can be spread from human to human by blood, so many countries have banned blood donation from regions associated with BSE.

The cause of spongiform encephalopathies, such as kuru and BSE, is an infectious structural variant of a normal cellular protein called PrP (prion protein). It is this variant that constitutes the prion particle. PrP exists in two forms, **PrP_c**, the normal form of the protein, and **PrP_{sc}**, the infectious form. Once introduced into the body, the PrP_{sc} contained within the prion binds to PrP_c and converts it to PrP_{sc}. This leads to an exponential increase of the PrP_{sc} protein, which aggregates. PrP_{sc} is folded abnormally, and the resulting conformation (shape) is directly responsible for the lesions seen in the brains of infected cattle. Thus, although not without some detractors among scientists, the prion seems likely to be an entirely new form of infectious agent, the first one found whose transmission is not reliant upon genes made of DNA or RNA.



These potatoes have been infected by the potato spindle tuber viroid (PSTV), which is typically spread when infected knives are used to cut healthy potatoes, which are then planted. (credit: Pamela Roberts, University of Florida Institute of Food and Agricultural Sciences, USDA ARS)

Viroids

Viroids are plant pathogens: small, single-stranded, circular RNA particles that are much simpler than a virus. They do not have a capsid or outer envelope, but like viruses can reproduce only within a host cell. Viroids do not, however, manufacture any proteins, and they only produce a single, specific RNA molecule. Human diseases caused by viroids have yet to be identified.

Viroids are known to infect plants ([link]) and are responsible for crop failures and the loss of millions of dollars in agricultural revenue each year. Some of the plants they infect include potatoes, cucumbers, tomatoes, chrysanthemums, avocados, and coconut

palms.

Career Connection

Virologist

Virology is the study of viruses, and a virologist is an individual trained in this discipline. Training in virology can lead to many different career paths. Virologists are actively involved in academic research and teaching in colleges and medical schools. Some virologists treat patients or are involved in the generation and production of vaccines. They might participate in epidemiologic studies ([link]) or become science writers, to name just a few possible careers.

This virologist is engaged in fieldwork, sampling eggs from this nest for avian influenza. (credit: Don

Becker, USGS EROS, U.S. Fish and Wildlife Service)

If you think you may be interested in a career in virology, find a mentor in the field. Many large medical centers have departments of virology, and smaller hospitals usually have virology labs within their microbiology departments. Volunteer in a virology lab for a semester or work in one over the summer. Discussing the profession and getting a first-hand look at the work will help you decide whether a career in virology is right for you. The American Society of Virology's website is a good

resource for information regarding training and careers in virology.

Section Summary

Prions are infectious agents that consist of protein, but no DNA or RNA, and seem to produce their deadly effects by duplicating their shapes and accumulating in tissues. They are thought to contribute to several progressive brain disorders, including mad cow disease and Creutzfeldt-Jakob disease. Viroids are single-stranded RNA pathogens that infect plants. Their presence can have a severe impact on the agriculture industry.

Review Questions

Which of the following is not associated with prions?

1. Replicating shapes
2. Mad cow disease
3. DNA
4. Toxic proteins

C

Which statement is true of viroids?

1. They are single-stranded RNA particles.
2. They reproduce only outside of the cell.
3. They produce proteins.
4. They affect both plants and animals.

A

Critical Thinking Questions

Prions are responsible for variant Creutzfeldt-Jakob Disease, which has resulted in over 100 human deaths in Great Britain during the last 10 years. How do humans contract this disease?

This prion-based disease is transmitted through human consumption of infected meat.

How are viroids like viruses?

They both replicate in a cell, and they both contain nucleic acid.

A botanist notices that a tomato plant looks diseased. How could the botanist confirm that the agent causing disease is a viroid, and not a virus?

The botanist would need to isolate any foreign nucleic acids from infected plant cells, and confirm that an RNA molecule is the etiological agent of disease. The botanist would then need to demonstrate that the RNA can infect plant cells without a capsid, and that the RNA replicates, but is not translated to produce proteins.

Glossary

pathogen
: agent with the ability to cause disease

prion
: infectious particle that consists of proteins that replicate without DNA or RNA

PrP_c
: normal prion protein

PrP^{Sc}
: infectious form of a prion protein

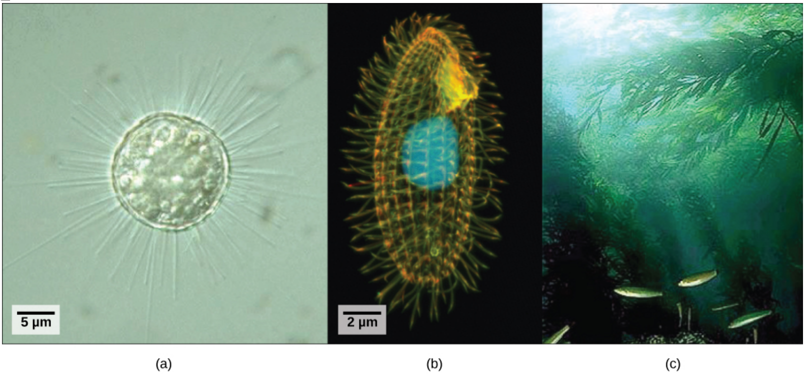
viroid
: plant pathogen that produces only a single, specific RNA

Protists

By the end of this section, you will be able to:

- Describe the main characteristics of protists
- Describe important pathogenic species of protists
- Describe the roles of protists as food sources and as decomposers

Protists range from the microscopic, single-celled (a) *Acanthocystis turfacea* and the (b) ciliate *Tetrahymena thermophila* to the enormous, multicellular (c) kelps (Chromalveolata) that extend for hundreds of feet in underwater "forests." (credit a: modification of work by Yuiuji Tsukii; credit b: modification of work by Richard Robinson, Public Library of Science; credit c: modification of work by Kip Evans, NOAA; scale-bar data from Matt Russell)



Eukaryotic organisms that did not fit the criteria for the kingdoms Animalia, Fungi, or Plantae historically were called protists and were classified

into the kingdom Protista. Protists include the single-celled eukaryotes living in pond water ([link]), although protist species live in a variety of other aquatic and terrestrial environments, and occupy many different niches. This name was first suggested by Ernst Haeckel in the late nineteenth century. It has been applied in many contexts and has been formally used to represent a kingdom-level taxon called Protista. During the past two decades, the field of molecular genetics has demonstrated that some protists are more related to animals, plants, or fungi than they are to other protists. For this reason, protist lineages originally classified into the kingdom Protista continue to be examined and debated. In the meantime, the term “protist” still is used informally to describe this tremendously diverse group of eukaryotes.

Most protists are microscopic, unicellular organisms that are abundant in soil, freshwater, brackish, and marine environments. They are also common in the digestive tracts of animals and in the vascular tissues of plants. Others invade the cells of other protists, animals, and plants. Not all protists are microscopic. Some have huge, macroscopic cells, such as the plasmodia (giant amoebae) of myxomycete slime molds or the marine green alga *Caulerpa*, which can have single cells that can be several meters in size. Some protists are multicellular, such as the red, green, and brown seaweeds. It is among the protists that one finds the

wealth of ways that organisms can grow.
Protists use various methods for transportation. (a) *Paramecium* waves hair-like appendages called cilia to propel itself. (b) *Amoeba* uses lobe-like pseudopodia to anchor itself to a solid surface and pull itself forward. (c) *Euglena* uses a whip-like tail called a flagellum to propel itself.

Characteristics of Protists

There are over 100,000 described living species of protists, and it is unclear how many undescribed species may exist. Since many protists live in symbiotic relationships with other organisms and these relationships are often species specific, there is a huge potential for undescribed protist diversity that matches the diversity of the hosts. As the catchall term for eukaryotic organisms that are not animals, plants, fungi, or any single phylogenetically related group, it is not surprising that few characteristics are common to all protists.

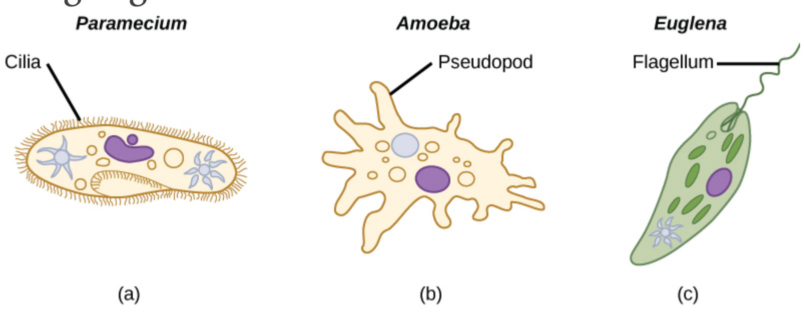
Habitats

Nearly all protists exist in some type of aquatic environment, including freshwater and marine environments, damp soil, and even snow. Several protist species are parasites that infect animals or plants. A few protist species live on dead organisms or their wastes, and contribute to their decay.

Protists function in various ecological niches. Whereas some protist species are essential components of the food chain and generators of biomass, others function in the decomposition of organic materials. Still other protists are dangerous human pathogens or causative agents of devastating plant diseases.

Motility

The majority of protists are motile, but different types of protists have evolved varied modes of movement ([link]). Some protists have one or more flagella, which they rotate or whip. Others are covered in rows or tufts of tiny cilia that they coordinately beat to swim. Still others form cytoplasmic extensions called pseudopodia anywhere on the cell, anchor the pseudopodia to a substrate, and pull themselves forward. Some protists can move toward or away from a stimulus, a movement referred to as taxis. Movement toward light, termed phototaxis, is accomplished by coupling their locomotion strategy with a light-sensing organ.



Protist Structure

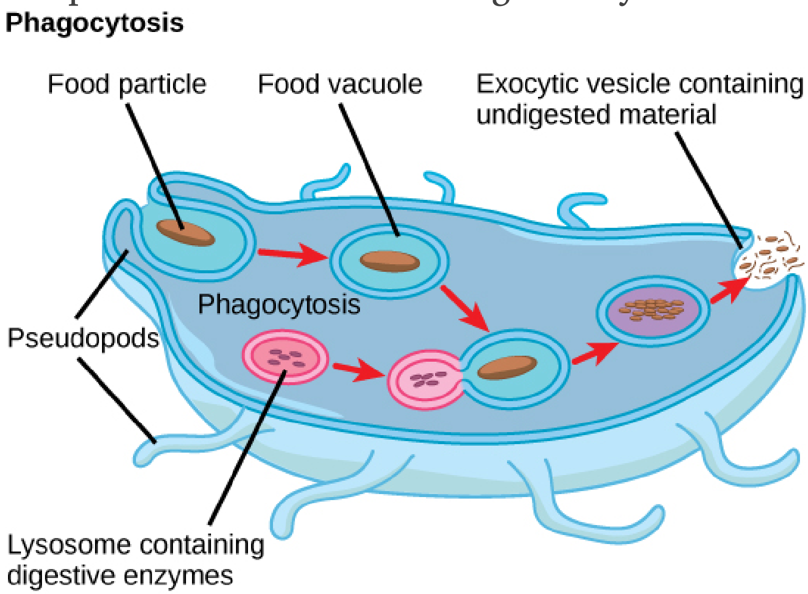
The cells of protists are among the most elaborate of all cells. Most protists are microscopic and unicellular, but some true multicellular forms exist. A few protists live as colonies that behave in some ways as a group of free-living cells and in other ways as a multicellular organism. Still other protists are composed of enormous, multinucleate, single cells that look like amorphous blobs of slime or, in other cases, like ferns. In fact, many protist cells are multinucleated; in some species, the nuclei are different sizes and have distinct roles in protist cell function.

Single protist cells range in size from less than a micrometer to the 3-meter lengths of the multinucleate cells of the seaweed *Caulerpa*. Protist cells may be enveloped by animal-like cell membranes or plant-like cell walls. Others are encased in glassy silica-based shells or wound with **pellicles** of interlocking protein strips. The pellicle functions like a flexible coat of armor, preventing the protist from being torn or pierced without compromising its range of motion.

The stages of phagocytosis include the engulfment of a food particle, the digestion of the particle using hydrolytic enzymes contained within a lysosome, and the expulsion of undigested material from the cell.

How Protists Obtain Energy

Protists exhibit many forms of nutrition and may be aerobic or anaerobic. Photosynthetic protists (photoautotrophs) are characterized by the presence of chloroplasts. Other protists are heterotrophs and consume organic materials (such as other organisms) to obtain nutrition. Amoebas and some other heterotrophic protist species ingest particles by a process called phagocytosis, in which the cell membrane engulfs a food particle and brings it inward, pinching off an intracellular membranous sac, or vesicle, called a food vacuole ([link]). This vesicle then fuses with a lysosome, and the food particle is broken down into small molecules that can diffuse into the cytoplasm and be used in cellular metabolism. Undigested remains ultimately are expelled from the cell through exocytosis.



Some heterotrophs absorb nutrients from dead organisms or their organic wastes, and others are able to use photosynthesis or feed on organic matter, depending on conditions.

Reproduction

Protists reproduce by a variety of mechanisms. Most are capable some form of asexual reproduction, such as binary fission to produce two daughter cells, or multiple fission to divide simultaneously into many daughter cells. Others produce tiny buds that go on to divide and grow to the size of the parental protist. Sexual reproduction, involving meiosis and fertilization, is common among protists, and many protist species can switch from asexual to sexual reproduction when necessary. Sexual reproduction is often associated with periods when nutrients are depleted or environmental changes occur. Sexual reproduction may allow the protist to recombine genes and produce new variations of progeny that may be better suited to surviving in the new environment. However, sexual reproduction is also often associated with cysts that are a protective, resting stage. Depending on their habitat, the cysts may be particularly resistant to temperature extremes, desiccation, or low pH. This strategy also allows certain protists to “wait out” stressors until their environment becomes more favorable for survival or until they are carried (such as by wind,

water, or transport on a larger organism) to a different environment because cysts exhibit virtually no cellular metabolism.

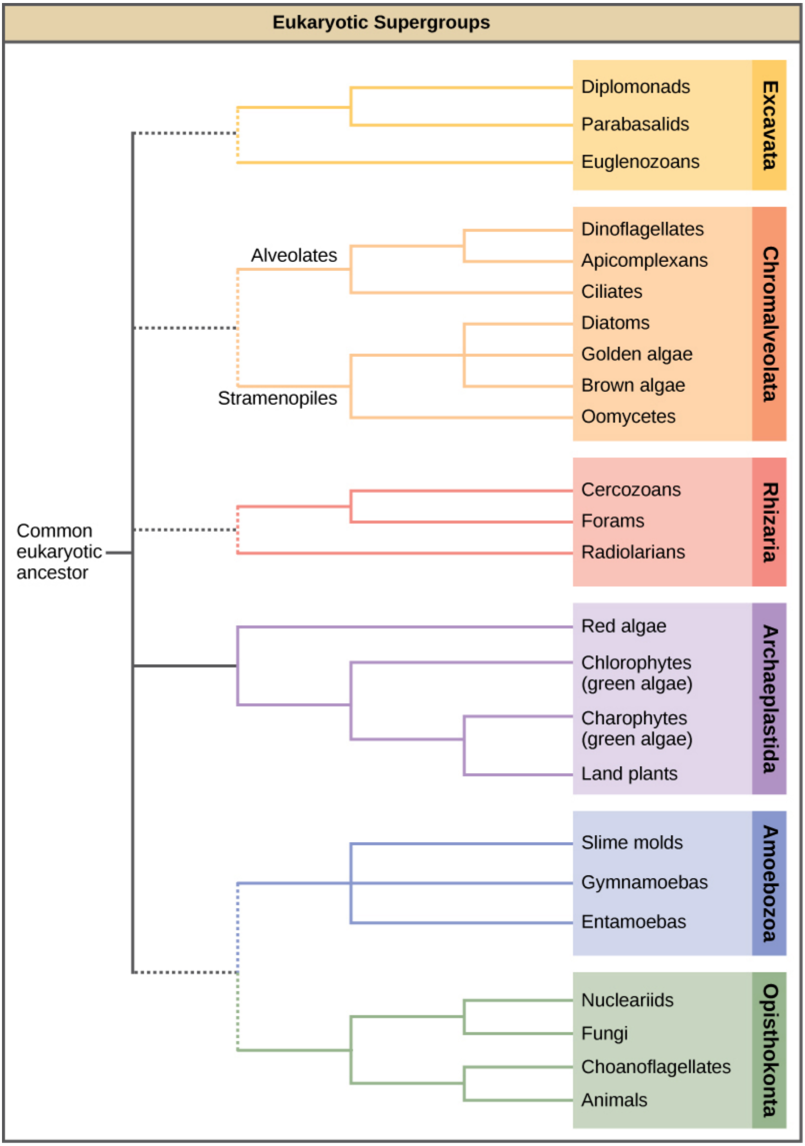
Protist life cycles range from simple to extremely elaborate. Certain parasitic protists have complicated life cycles and must infect different host species at different developmental stages to complete their life cycle. Some protists are unicellular in the haploid form and multicellular in the diploid form, a strategy employed by animals. Other protists have multicellular stages in both haploid and diploid forms, a strategy called alternation of generations that is also used by plants.

Protists appear in all six eukaryotic supergroups.

Protist Diversity

With the advent of DNA sequencing, the relationships among protist groups and between protist groups and other eukaryotes are beginning to become clearer. Many relationships that were based on morphological similarities are being replaced by new relationships based on genetic similarities. Protists that exhibit similar morphological features may have evolved analogous structures because of similar selective pressures—rather than because of recent common ancestry. This phenomenon is called convergent evolution. It is one reason why protist classification is so challenging. The emerging

classification scheme groups the entire domain Eukaryota into six “supergroups” that contain all of the protists as well as animals, plants, and fungi ([link]); these include the **Excavata**, **Chromalveolata**, **Rhizaria**, **Archaeplastida**, **Amoebozoa**, and **Opisthokonta**. The supergroups are believed to be monophyletic; all organisms within each supergroup are believed to have evolved from a single common ancestor, and thus all members are most closely related to each other than to organisms outside that group. There is still evidence lacking for the monophyly of some groups.



This light micrograph shows a 100× magnification of red blood cells infected with *P. falciparum* (seen as purple). (credit: modification of work by Michael Zahniser; scale-bar data from Matt Russell) Trypanosomes are shown in this light micrograph among red blood cells. (credit: modification of work

by Myron G. Schultz, CDC; scale-bar data from Matt Russell)

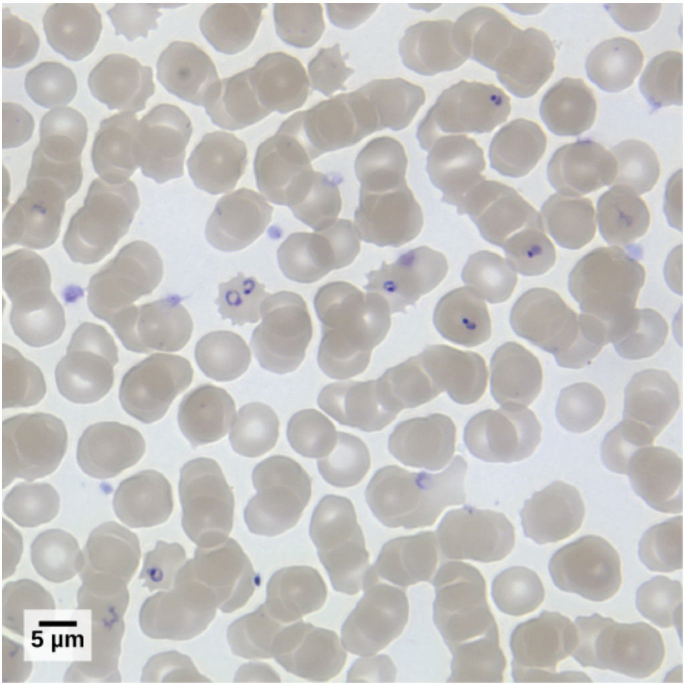
Human Pathogens

Many protists are pathogenic parasites that must infect other organisms to survive and propagate. Protist parasites include the causative agents of malaria, African sleeping sickness, and waterborne gastroenteritis in humans. Other protist pathogens prey on plants, effecting massive destruction of food crops.

Plasmodium Species

Members of the genus *Plasmodium* must infect a mosquito and a vertebrate to complete their life cycle. In vertebrates, the parasite develops in liver cells and goes on to infect red blood cells, bursting from and destroying the blood cells with each asexual replication cycle ([link]). Of the four *Plasmodium* species known to infect humans, *P. falciparum* accounts for 50 percent of all malaria cases and is the primary cause of disease-related fatalities in tropical regions of the world. In 2010, it was estimated that malaria caused between 0.5 and 1 million deaths, mostly in African children. During the course of malaria, *P. falciparum* can infect and destroy more than one-half of a human's circulating blood cells, leading to severe anemia. In response to

waste products released as the parasites burst from infected blood cells, the host immune system mounts a massive inflammatory response with delirium-inducing fever episodes, as parasites destroy red blood cells, spilling parasite waste into the blood stream. *P. falciparum* is transmitted to humans by the African malaria mosquito, *Anopheles gambiae*. Techniques to kill, sterilize, or avoid exposure to this highly aggressive mosquito species are crucial to malaria control.



Concept in Action

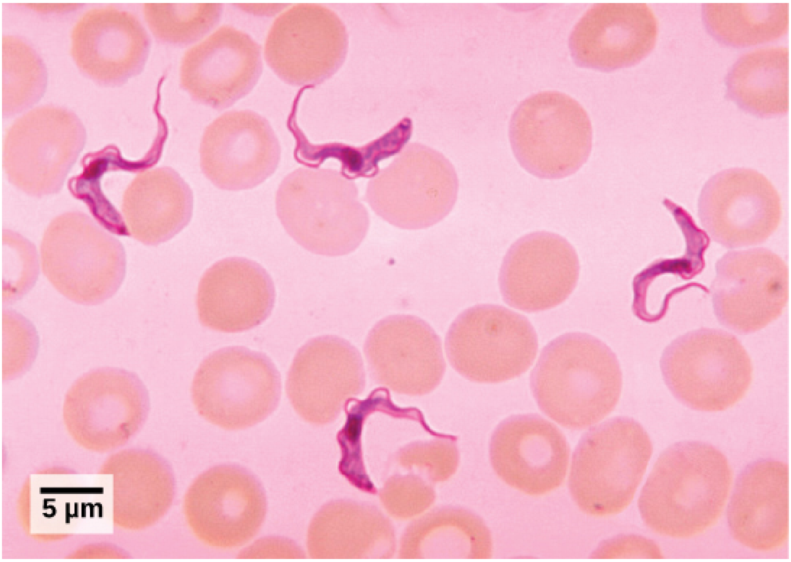
This movie depicts the pathogenesis of *Plasmodium falciparum*, the causative agent of malaria.

Trypanosomes

T. brucei, the parasite that is responsible for African sleeping sickness, confounds the human immune system by changing its thick layer of surface glycoproteins with each infectious cycle ([link]). The glycoproteins are identified by the immune system as foreign matter, and a specific antibody defense is mounted against the parasite. However, *T. brucei* has thousands of possible antigens, and with each subsequent generation, the protist switches to a glycoprotein coating with a different molecular structure. In this way, *T. brucei* is capable of replicating continuously without the immune system ever succeeding in clearing the parasite. Without treatment, African sleeping sickness leads invariably to death because of damage it does to the nervous system. During epidemic periods, mortality from the disease can be high. Greater surveillance and control measures have led to a reduction in

reported cases; some of the lowest numbers reported in 50 years (fewer than 10,000 cases in all of sub-Saharan Africa) have happened since 2009.

In Latin America, another species in the genus, *T. cruzi*, is responsible for Chagas disease. *T. cruzi* infections are mainly caused by a blood-sucking bug. The parasite inhabits heart and digestive system tissues in the chronic phase of infection, leading to malnutrition and heart failure caused by abnormal heart rhythms. An estimated 10 million people are infected with Chagas disease, which caused 10,000 deaths in 2008.



Concept in Action

This movie discusses the pathogenesis of *Trypanosoma brucei*, the causative agent of African sleeping sickness.

(a) The downy and powdery mildews on this grape leaf are caused by an infection of *P. viticola*. (b) This potato exhibits the results of an infection with *P. infestans*, the potato late blight. (credit a: modification of work by David B. Langston, University of Georgia, USDA ARS; credit b: USDA ARS)

Plant Parasites

Protist parasites of terrestrial plants include agents that destroy food crops. The oomycete *Plasmopara viticola* parasitizes grape plants, causing a disease called downy mildew ([link]**a**). Grape plants infected with *P. viticola* appear stunted and have discolored withered leaves. The spread of downy mildew caused the near collapse of the French wine industry in the nineteenth century.

(a) (b)

Phytophthora infestans is an oomycete responsible for potato late blight, which causes potato stalks and stems to decay into black slime ([link]**b**). Widespread potato blight caused by *P. infestans* precipitated the well-known Irish potato famine in the nineteenth century that claimed the lives of approximately 1 million people and led to the emigration from Ireland of at least 1 million more. Late blight continues to plague potato crops in certain parts of the United States and Russia, wiping out as much as 70 percent of crops when no pesticides are applied.

Coral polyps obtain nutrition through a symbiotic relationship with dinoflagellates.Virtually all aquatic organisms depend directly or indirectly on protists for food. (credit “mollusks”: modification of work by Craig Stihler, USFWS; credit “crab”: modification of work by David Berkowitz; credit “dolphin”: modification of work by Mike Baird; credit “fish”: modification of work by Tim Sheerman-Chase; credit “penguin”: modification of work by Aaron Logan)

Beneficial Protists

Protists play critically important ecological roles as producers particularly in the world's oceans. They are equally important on the other end of food webs as decomposers.

Protists as Food Sources

Protists are essential sources of nutrition for many other organisms. In some cases, as in plankton, protists are consumed directly. Alternatively, photosynthetic protists serve as producers of nutrition for other organisms by carbon fixation. For instance, photosynthetic dinoflagellates called zooxanthellae pass on most of their energy to the coral polyps that house them ([link]). In this mutually beneficial relationship, the polyps provide a protective environment and nutrients for the zooxanthellae. The polyps secrete the calcium carbonate that builds coral reefs. Without dinoflagellate symbionts, corals lose algal pigments in a process called coral bleaching, and they eventually die. This explains why reef-building corals do not reside in waters deeper than 20 meters: Not enough light reaches those depths for dinoflagellates to photosynthesize.

The protists themselves and their products of photosynthesis are essential—directly or indirectly—to the survival of organisms ranging from bacteria to mammals ([link]). As primary producers, protists feed a large proportion of the world’s aquatic species. (On land, terrestrial plants serve as primary producers.) In fact, approximately one-quarter of the world’s photosynthesis is conducted by protists, particularly dinoflagellates, diatoms, and multicellular algae.

Protists do not create food sources only for sea-dwelling organisms. For instance, certain anaerobic species exist in the digestive tracts of termites and wood-eating cockroaches, where they contribute to digesting cellulose ingested by these insects as they bore through wood. The actual enzyme used to digest the cellulose is actually produced by bacteria

living within the protist cells. The termite provides the food source to the protist and its bacteria, and the protist and bacteria provide nutrients to the termite by breaking down the cellulose.

Agents of Decomposition

Many fungus-like protists are **saprobes**, organisms that feed on dead organisms or the waste matter produced by organisms (saprophyte is an equivalent term), and are specialized to absorb nutrients from nonliving organic matter. For instance, many types of oomycetes grow on dead animals or algae. Saprobic protists have the essential function of returning inorganic nutrients to the soil and water. This process allows for new plant growth, which in turn generates sustenance for other organisms along the food chain. Indeed, without saprobic species, such as protists, fungi, and bacteria, life would cease to exist as all organic carbon became “tied up” in dead organisms.

Section Summary

Protists are extremely diverse in terms of biological and ecological characteristics due in large part to the fact that they are an artificial assemblage of phylogenetically unrelated groups. Protists display highly varied cell structures, several types of

reproductive strategies, virtually every possible type of nutrition, and varied habitats. Most single-celled protists are motile, but these organisms use diverse structures for transportation.

The process of classifying protists into meaningful groups is ongoing, but genetic data in the past 20 years have clarified many relationships that were previously unclear or mistaken. The majority view at present is to order all eukaryotes into six supergroups. The goal of this classification scheme is to create clusters of species that all are derived from a common ancestor.

Review Questions

Protists that have a pellicle are surrounded by __________.

1. silica dioxide
2. calcium carbonate
3. carbohydrates
4. proteins

D

Protists with the capabilities to perform

photosynthesis and to absorb nutrients from dead organisms are called _________.

1. photoautotrophs
2. mixotrophs
3. saprobes
4. heterotrophs

B

Which of these locomotor organs would likely be the shortest?

1. a flagellum
2. a cilium
3. an extended pseudopod
4. a pellicle

B

Which parasitic protist evades the host immune system by altering its surface proteins with each generation?

1. *Paramecium caudatum*
2. *Trypanosoma brucei*
3. *Plasmodium falciparum*
4. *Phytophthora infestans*

B

Free Response

Explain in your own words why sexual reproduction can be useful if a protist's environment changes.

The ability to perform sexual reproduction allows protists to recombine their genes and produce new variations of progeny that may be better suited to the new environment. In contrast, asexual reproduction generates progeny that are clones of the parent.

How does killing *Anopheles* mosquitoes affect the *Plasmodium* protists?

Plasmodium parasites infect humans and cause malaria. However, they must complete part of their life cycle within *Anopheles* mosquitoes, and they can only be transmitted to humans via the bite wound of a mosquito. If the mosquito population were decreased, then fewer *Plasmodium* would be able to develop and be

transmitted to humans, thereby reducing the incidence of human infections with this parasite.

Without treatment, why does African sleeping sickness invariably lead to death?

The trypanosomes that cause this disease are capable of expressing a glycoprotein coat with a different molecular structure with each generation. Because the immune system must respond to specific antigens to raise a meaningful defense, the changing nature of trypanosome antigens prevents the immune system from ever clearing this infection. Massive trypanosome infection eventually leads to host organ failure and death.

Glossary

Amoebozoa
: the eukaryotic supergroup that contains the amoebas and slime molds

Archaeplastida
: the eukaryotic supergroup that contains land plants, green algae, and red algae

Chromalveolata

the eukaryotic supergroup that contains the dinoflagellates, ciliates, the brown algae, diatoms, and water molds

Excavata
: the eukaryotic supergroup that contains flagellated single-celled organisms with a feeding groove

Opisthokonta
: the eukaryotic supergroup that contains the fungi, animals, and choanoflagellates

parasite
: an organism that lives on or in another organism and feeds on it, often without killing it

pellicle
: an outer cell covering composed of interlocking protein strips that function like a flexible coat of armor, preventing cells from being torn or pierced without compromising their range of motion

Rhizaria
: the eukaryotic supergroup that contains organisms that move by amoeboid movement

saprobe
: an organism that feeds on dead organic material

Early Plant Life

By the end of this section, you will be able to:

- Describe the major characteristics of the plant kingdom
- Discuss the challenges to plant life on land
- Describe the adaptations that allowed plants to colonize land

Plants are a large and varied group of organisms. There are close to 300,000 species of catalogued plants.[footnote] Of these, about 260,000 are plants that produce seeds. Mosses, ferns, conifers, and flowering plants are all members of the plant kingdom. The plant kingdom contains mostly photosynthetic organisms; a few parasitic forms have lost the ability to photosynthesize. The process of photosynthesis uses chlorophyll, which is located in organelles called chloroplasts. Plants possess cell walls containing cellulose. Most plants reproduce sexually, but they also have diverse methods of asexual reproduction. Plants exhibit indeterminate growth, meaning they do not have a final body form, but continue to grow body mass until they die.

A.D. Chapman (2009) *Numbers of Living Species in Australia and the World*. 2nd edition. A Report for the Australian Biological Resources Study. Australian Biodiversity Information Services, Toowoomba, Australia. Available online at http://www.environment.gov.au/biodiversity/abrs/

publications/other/species-numbers/2009/04-03-groups-plants.html. Alternation of generations between the haploid ($1n$) gametophyte and diploid ($2n$) sporophyte is shown. (credit: modification of work by Peter Coxhead) This life cycle of a fern shows alternation of generations with a dominant sporophyte stage. (credit "fern": modification of work by Cory Zanker; credit "gametophyte": modification of work by "Vlmastra"/Wikimedia Commons) This life cycle of a moss shows alternation of generations with a dominant gametophyte stage. (credit: modification of work by Mariana Ruiz Villareal) This apple seedling is an example of a plant in which the apical meristem gives rise to new shoots and root growth.

Plant Adaptations to Life on Land

As organisms adapt to life on land, they have to contend with several challenges in the terrestrial environment. Water has been described as "the stuff of life." The cell's interior—the medium in which most small molecules dissolve and diffuse, and in which the majority of the chemical reactions of metabolism take place—is a watery soup. Desiccation, or drying out, is a constant danger for an organism exposed to air. Even when parts of a plant are close to a source of water, their aerial structures are likely to dry out. Water provides buoyancy to organisms that live in aquatic habitats. On land, plants need to develop structural support

in air—a medium that does not give the same lift. Additionally, the male gametes must reach the female gametes using new strategies because swimming is no longer possible. Finally, both gametes and zygotes must be protected from drying out. The successful land plants evolved strategies to deal with all of these challenges, although not all adaptations appeared at once. Some species did not move far from an aquatic environment, whereas others left the water and went on to conquer the driest environments on Earth.

To balance these survival challenges, life on land offers several advantages. First, sunlight is abundant. On land, the spectral quality of light absorbed by the photosynthetic pigment, chlorophyll, is not filtered out by water or competing photosynthetic species in the water column above. Second, carbon dioxide is more readily available because its concentration is higher in air than in water. Additionally, land plants evolved before land animals; therefore, until dry land was colonized by animals, no predators threatened the well-being of plants. This situation changed as animals emerged from the water and found abundant sources of nutrients in the established flora. In turn, plants evolved strategies to deter predation: from spines and thorns to toxic chemicals.

The early land plants, like the early land animals,

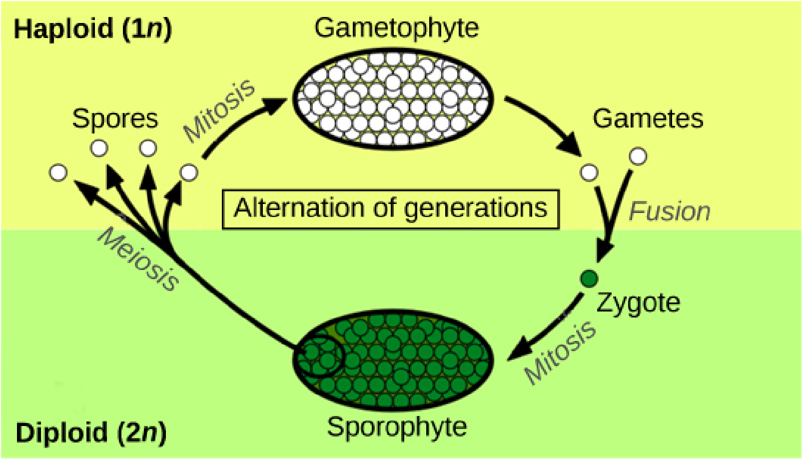
did not live far from an abundant source of water and developed survival strategies to combat dryness. One of these strategies is drought tolerance. Mosses, for example, can dry out to a brown and brittle mat, but as soon as rain makes water available, mosses will soak it up and regain their healthy, green appearance. Another strategy is to colonize environments with high humidity where droughts are uncommon. Ferns, an early lineage of plants, thrive in damp and cool places, such as the understory of temperate forests. Later, plants moved away from aquatic environments using resistance to desiccation, rather than tolerance. These plants, like the cactus, minimize water loss to such an extent they can survive in the driest environments on Earth.

In addition to adaptations specific to life on land, land plants exhibit adaptations that were responsible for their diversity and predominance in terrestrial ecosystems. Four major adaptations are found in many terrestrial plants: the alternation of generations, a sporangium in which spores are formed, a gametangium that produces haploid cells, and in vascular plants, apical meristem tissue in roots and shoots.

Alternation of Generations

Alternation of generations describes a life cycle in which an organism has both haploid and diploid

multicellular stages ([link]).



Haplontic refers to a life cycle in which there is a dominant haploid stage. **Diplontic** refers to a life cycle in which the diploid stage is the dominant stage, and the haploid chromosome number is only seen for a brief time in the life cycle during sexual reproduction. Humans are diplontic, for example. Most plants exhibit alternation of generations, which is described as **haplodiplontic**: the haploid multicellular form known as a gametophyte is followed in the development sequence by a multicellular diploid organism, the **sporophyte**. The **gametophyte** gives rise to the gametes, or reproductive cells, by mitosis. It can be the most obvious phase of the life cycle of the plant, as in the mosses, or it can occur in a microscopic structure, such as a pollen grain in the higher plants (the collective term for the vascular plants). The sporophyte stage is barely noticeable in lower plants (the collective term for the plant groups of mosses,

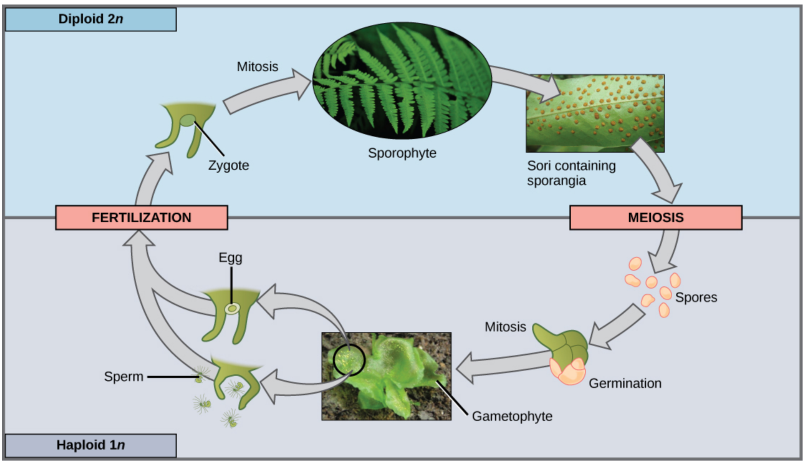
liverworts, and hornworts). Towering trees are the diplontic phase in the lifecycles of plants such as sequoias and pines.

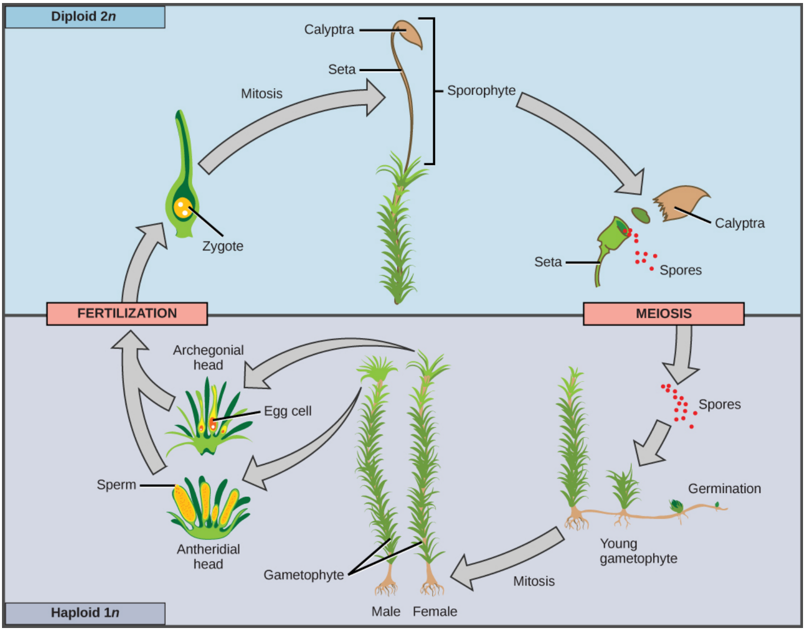
Sporangia in the Seedless Plants

The sporophyte of seedless plants is diploid and results from **syngamy** or the fusion of two gametes ([link]). The sporophyte bears the **sporangia** (singular, sporangium), organs that first appeared in the land plants. The term “sporangia” literally means “spore in a vessel,” as it is a reproductive sac that contains spores. Inside the multicellular sporangia, the diploid sporocytes, or mother cells, produce haploid spores by meiosis, which reduces the 2*n* chromosome number to 1*n*. The spores are later released by the sporangia and disperse in the environment. Two different types of spores are produced in land plants, resulting in the separation of sexes at different points in the life cycle. Seedless nonvascular plants (more appropriately referred to as “seedless nonvascular plants with a dominant gametophyte phase”) produce only one kind of spore, and are called **homosporous**. After germinating from a spore, the gametophyte produces both male and female **gametangia**, usually on the same individual. In contrast, **heterosporous** plants produce two morphologically different types of spores. The male spores are called microspores because of their smaller size; the comparatively larger megaspores will develop into

the female gametophyte. Heterospory is observed in a few seedless vascular plants and in all seed plants.

When the haploid spore germinates, it generates a multicellular gametophyte by mitosis. The gametophyte supports the zygote formed from the fusion of gametes and the resulting young sporophyte or vegetative form, and the cycle begins anew ([link] and [link]).





The spores of seedless plants and the pollen of seed plants are surrounded by thick cell walls containing a tough polymer known as sporopollenin. This substance is characterized by long chains of organic molecules related to fatty acids and carotenoids, and gives most pollen its yellow color. Sporopollenin is unusually resistant to chemical and biological degradation. Its toughness explains the existence of well-preserved fossils of pollen. Sporopollenin was once thought to be an innovation of land plants; however, the green algae *Coleochaetes* is now known to form spores that contain sporopollenin.

Protection of the embryo is a major requirement for land plants. The vulnerable embryo must be sheltered from desiccation and other environmental

hazards. In both seedless and seed plants, the female gametophyte provides nutrition, and in seed plants, the embryo is also protected as it develops into the new generation of sporophyte.

Gametangia in the Seedless Plants

Gametangia (singular, gametangium) are structures on the gametophytes of seedless plants in which gametes are produced by mitosis. The male gametangium, the antheridium, releases sperm. Many seedless plants produce sperm equipped with flagella that enable them to swim in a moist environment to the archegonia, the female gametangium. The embryo develops inside the archegonium as the sporophyte.

Apical Meristems

The shoots and roots of plants increase in length through rapid cell division within a tissue called the **apical meristem** ([link]). The apical meristem is a cap of cells at the shoot tip or root tip made of undifferentiated cells that continue to proliferate throughout the life of the plant. Meristematic cells give rise to all the specialized tissues of the plant. Elongation of the shoots and roots allows a plant to access additional space and resources: light in the case of the shoot, and water and minerals in the case of roots. A separate meristem, called the lateral meristem, produces cells that increase the diameter

of stems and tree trunks. Apical meristems are an adaptation to allow vascular plants to grow in directions essential to their survival: upward to greater availability of sunlight, and downward into the soil to obtain water and essential minerals.

Plants have evolved various adaptations to life on land. (a) Early plants grew close to the ground, like this moss, to avoid desiccation. (b) Later plants developed a waxy cuticle to prevent desiccation. (c) To grow taller, like these maple trees, plants had to evolve new structural chemicals to strengthen their stems and vascular systems to transport water and minerals from the soil and nutrients from the leaves.

(d) Plants developed physical and chemical defenses to avoid being eaten by animals. (credit a, b: modification of work by Cory Zanker; credit c: modification of work by Christine Cimala; credit d: modification of work by Jo Naylor)

Additional Land Plant Adaptations

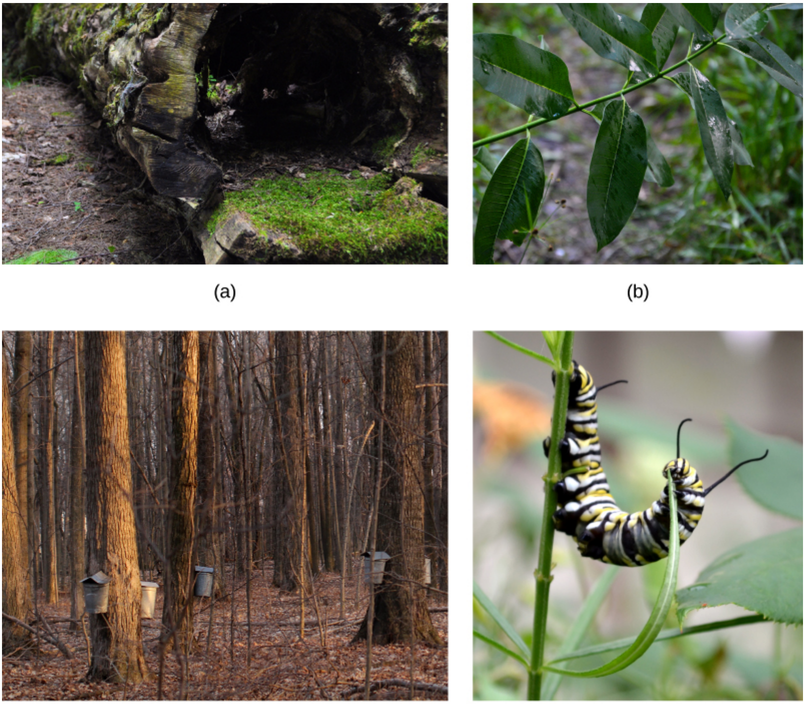
As plants adapted to dry land and became independent of the constant presence of water in damp habitats, new organs and structures made their appearance. Early land plants did not grow above a few inches off the ground, and on these low mats, they competed for light. By evolving a shoot and growing taller, individual plants captured more light. Because air offers substantially less support than water, land plants incorporated more rigid molecules in their stems (and later, tree trunks). The evolution of vascular tissue for the distribution of water and solutes was a necessary prerequisite for plants to evolve larger bodies. The vascular system contains xylem and phloem tissues. Xylem conducts water and minerals taken from the soil up to the shoot; phloem transports food derived from photosynthesis throughout the entire plant. The root system that evolved to take up water and minerals also anchored the increasingly taller shoot in the soil.

In land plants, a waxy, waterproof cover called a cuticle coats the aerial parts of the plant: leaves and

stems. The cuticle also prevents intake of carbon dioxide needed for the synthesis of carbohydrates through photosynthesis. Stomata, or pores, that open and close to regulate traffic of gases and water vapor therefore appeared in plants as they moved into drier habitats.

Plants cannot avoid predatory animals. Instead, they synthesize a large range of poisonous secondary metabolites: complex organic molecules such as alkaloids, whose noxious smells and unpleasant taste deter animals. These toxic compounds can cause severe diseases and even death.

Additionally, as plants coevolved with animals, sweet and nutritious metabolites were developed to lure animals into providing valuable assistance in dispersing pollen grains, fruit, or seeds. Plants have been coevolving with animal associates for hundreds of millions of years ([link]).



(a) (b) (c) (d)

Evolution in Action

Paleobotany

How organisms acquired traits that allow them to colonize new environments, and how the contemporary ecosystem is shaped, are fundamental questions of evolution. Paleobotany addresses these questions by specializing in the study of extinct plants. Paleobotanists analyze specimens retrieved from field studies, reconstituting the morphology of organisms that have long disappeared. They trace the evolution of plants by following the modifications in plant

morphology, and shed light on the connection between existing plants by identifying common ancestors that display the same traits. This field seeks to find transitional species that bridge gaps in the path to the development of modern organisms. Fossils are formed when organisms are trapped in sediments or environments where their shapes are preserved ([link]). Paleobotanists determine the geological age of specimens and the nature of their environment using the geological sediments and fossil organisms surrounding them. The activity requires great care to preserve the integrity of the delicate fossils and the layers in which they are found.

One of the most exciting recent developments in paleobotany is the use of analytical chemistry and molecular biology to study fossils. Preservation of molecular structures requires an environment free of oxygen, since oxidation and degradation of material through the activity of microorganisms depend on the presence of oxygen. One example of the use of analytical chemistry and molecular biology is in the identification of oleanane, a compound that deters pests and which, up to this point, appears to be unique to flowering plants. Oleanane was recovered from sediments dating from the Permian, much earlier than the current dates given for the appearance of the first flowering plants. Fossilized nucleic acids—DNA and RNA—yield the most information. Their sequences are analyzed and compared to those of

living and related organisms. Through this analysis, evolutionary relationships can be built for plant lineages.

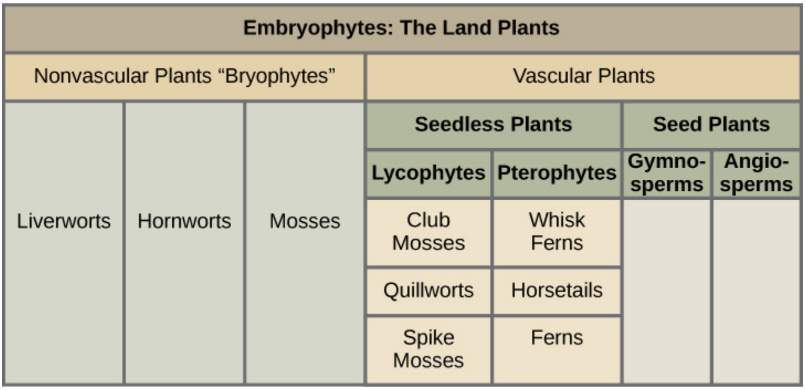
Some paleobotanists are skeptical of the conclusions drawn from the analysis of molecular fossils. For one, the chemical materials of interest degrade rapidly during initial isolation when exposed to air, as well as in further manipulations. There is always a high risk of contaminating the specimens with extraneous material, mostly from microorganisms. Nevertheless, as technology is refined, the analysis of DNA from fossilized plants will provide invaluable information on the evolution of plants and their adaptation to an ever-changing environment.

This fossil of a palm leaf (*Palmacites* sp.) discovered in Wyoming dates to about 40 million years ago.

This table shows the major divisions of plants.

The Major Divisions of Land Plants

Land plants are classified into two major groups according to the absence or presence of vascular tissue, as detailed in [link]. Plants that lack vascular tissue formed of specialized cells for the transport of water and nutrients are referred to as **nonvascular plants**. The bryophytes, liverworts, mosses, and hornworts are seedless and nonvascular, and likely appeared early in land plant evolution. **Vascular plants** developed a network of cells that conduct water and solutes through the plant body. The first vascular plants appeared in the late Ordovician (461–444 million years ago) and were probably similar to lycophytes, which include club mosses (not to be confused with the mosses) and the pterophytes (ferns, horsetails, and whisk ferns). Lycophytes and pterophytes are referred to as seedless vascular plants. They do not produce seeds, which are embryos with their stored food reserves protected by a hard casing. The seed plants form the largest group of all existing plants and, hence, dominate the landscape. Seed plants include gymnosperms, most notably conifers, which produce “naked seeds,” and the most successful plants, the flowering plants, or angiosperms, which protect their seeds inside chambers at the center of a flower. The walls of these chambers later develop into fruits.



Section Summary

Land plants evolved traits that made it possible to colonize land and survive out of water. Adaptations to life on land include vascular tissues, roots, leaves, waxy cuticles, and a tough outer layer that protects the spores. Land plants include nonvascular plants and vascular plants. Vascular plants, which include seedless plants and plants with seeds, have apical meristems, and embryos with nutritional stores. All land plants share the following characteristics: alternation of generations, with the haploid plant called a gametophyte and the diploid plant called a sporophyte; formation of haploid spores in a sporangium; and formation of gametes in a gametangium.

Multiple Choice

The land plants are probably descendants of which of these groups?

1. green algae
2. red algae
3. brown algae
4. angiosperms

A

The event that leads from the haploid stage to the diploid stage in alternation of generations is ______.

1. meiosis
2. mitosis
3. fertilization
4. germination

C

Moss is an example of which type of plant?

1. haplontic plant
2. vascular plant
3. diplontic plant
4. seed plant

A

Free Response

What adaptations do plants have that allow them to survive on land?

The sporangium of plants protects the spores from drying out. Apical meristems ensure that a plant is able to grow in the two directions required to acquire water and nutrients: up toward sunlight and down into the soil. The multicellular embryo is an important adaptation that improves survival of the developing plant in dry environments. The development of molecules that gave plants structural strength allowed them to grow higher on land and obtain more sunlight. A waxy cuticle prevents water loss from aerial surfaces.

Glossary

apical meristem
: the growing point in a vascular plant at the tip of a shoot or root where cell division occurs

diplontic
: describes a life cycle in which the diploid stage is the dominant stage

gametangium
: (plural: gametangia) the structure within which gametes are produced

gametophyte
: the haploid plant that produces gametes

haplodiplontic
: describes a life cycle in which the haploid and diploid stages alternate; also known as an alternation of generations life cycle

haplontic
: describes a life cycle in which the haploid stage is the dominant stage

heterosporous
: having two kinds of spores that give rise to male and female gametophytes

homosporous
: having one kind of spore that gives rise to gametophytes that give rise to both male and female gametes

nonvascular plant
: a plant that lacks vascular tissue formed of specialized cells for the transport of water and

nutrients

sporangium
(plural: sporangia) the organ within which spores are produced

sporophyte
the diploid plant that produces spores

syngamy
the union of two gametes in fertilization

vascular plant
a plant in which there is a network of cells that conduct water and solutes through the organism

Seedless Plants

By the end of this section, you will be able to:

- Describe the distinguishing traits of the three types of bryophytes
- Identify the new traits that first appear in seedless vascular plants
- Describe the major classes of seedless vascular plants

An incredible variety of seedless plants populates the terrestrial landscape. Mosses grow on tree trunks, and horsetails ([link]) display their jointed stems and spindly leaves on the forest floor. Yet, seedless plants represent only a small fraction of the plants in our environment. Three hundred million years ago, seedless plants dominated the landscape and grew in the enormous swampy forests of the Carboniferous period. Their decomposing bodies created large deposits of coal that we mine today.

Seedless plants like these horsetails (*Equisetum* sp.) thrive in damp, shaded environments under the tree canopy where dryness is a rare occurrence. (credit: Jerry Kirkhart)

Bryophytes

Bryophytes, an informal grouping of the nonvascular plants, are the closest extant relative of early terrestrial plants. The first bryophytes most probably appeared in the Ordovician period, about 490 million years ago. Because of the lack of lignin—the tough polymer in cell walls in the stems of vascular plants—and other resistant structures, the likelihood of bryophytes forming fossils is rather small, though some spores made up of sporopollenin have been discovered that have been attributed to early bryophytes. By the Silurian period (440 million years ago), however, vascular plants had spread throughout the continents. This fact is used as evidence that nonvascular plants must have preceded the Silurian period.

There are about 18,000 species of bryophytes, which thrive mostly in damp habitats, although some grow in deserts. They constitute the major flora of inhospitable environments like the tundra, where their small size and tolerance to desiccation offer distinct advantages. They do not have the specialized cells that conduct fluids found in the vascular plants, and generally lack lignin. In bryophytes, water and nutrients circulate inside specialized conducting cells. Although the name nontracheophyte is more accurate, bryophytes are commonly referred to as nonvascular plants.

In a bryophyte, all the conspicuous vegetative organs belong to the haploid organism, or gametophyte. The diploid sporophyte is barely noticeable. The gametes formed by bryophytes swim using flagella. The sporangium, the multicellular sexual reproductive structure, is present in bryophytes. The embryo also remains attached to the parent plant, which nourishes it. This is a characteristic of land plants.

The bryophytes are divided into three divisions (in plants, the taxonomic level “division” is used instead of phylum): the liverworts, or Marchantiophyta; the hornworts, or Anthocerotophyta; and the mosses, or true Bryophyta.
(a) A 1904 drawing of liverworts shows the variety of their forms. (b) A liverwort, *Lunularia cruciata*,

displays its lobate, flat thallus. The organism in the photograph is in the gametophyte stage.

Liverworts

Liverworts (Marchantiophyta) may be viewed as the plants most closely related to the ancestor that moved to land. Liverworts have colonized many habitats on Earth and diversified to more than 6,000 existing species ([link]**a**). Some gametophytes form lobate green structures, as seen in [link]**b**. The shape is similar to the lobes of the liver and, hence, provides the origin of the common name given to the division.

Hornworts grow a tall and slender sporophyte. (credit: modification of work by Jason Hollinger)

Hornworts

The **hornworts** (Anthocerotophyta) have colonized a variety of habitats on land, although they are never far from a source of moisture. There are about 100 described species of hornworts. The dominant phase of the life cycle of hornworts is the short, blue-green gametophyte. The sporophyte is the defining characteristic of the group. It is a long and narrow pipe-like structure that emerges from the parent gametophyte and maintains growth throughout the life of the plant ([link]).

This green feathery moss has reddish-brown sporophytes growing upward. (credit: "Lordgrunt"/ Wikimedia Commons)

Mosses

More than 12,000 species of **mosses** have been catalogued. Their habitats vary from the tundra, where they are the main vegetation, to the understory of tropical forests. In the tundra, their shallow rhizoids allow them to fasten to a substrate without digging into the frozen soil. They slow down erosion, store moisture and soil nutrients, and provide shelter for small animals and food for larger herbivores, such as the musk ox. Mosses are very sensitive to air pollution and are used to monitor the quality of air. The sensitivity of mosses to copper salts makes these salts a common ingredient of compounds marketed to eliminate mosses in lawns ([link]).

Vascular Plants

The vascular plants are the dominant and most conspicuous group of land plants. There are about 275,000 species of vascular plants, which represent more than 90 percent of Earth's vegetation. Several evolutionary innovations explain their success and their spread to so many habitats.

Vascular Tissue: Xylem and Phloem

The first fossils that show the presence of vascular tissue are dated to the Silurian period, about 430 million years ago. The simplest arrangement of conductive cells shows a pattern of xylem at the center surrounded by phloem. **Xylem** is the tissue responsible for long-distance transport of water and minerals, the transfer of water-soluble growth factors from the organs of synthesis to the target organs, and storage of water and nutrients.

A second type of vascular tissue is **phloem**, which transports sugars, proteins, and other solutes through the plant. Phloem cells are divided into sieve elements, or conducting cells, and supportive tissue. Together, xylem and phloem tissues form the vascular system of plants.

Roots: Support for the Plant

Roots are not well preserved in the fossil record; nevertheless, it seems that they did appear later in evolution than vascular tissue. The development of

an extensive network of roots represented a significant new feature of vascular plants. Thin rhizoids attached the bryophytes to the substrate. Their rather flimsy filaments did not provide a strong anchor for the plant; neither did they absorb water and nutrients. In contrast, roots, with their prominent vascular tissue system, transfer water and minerals from the soil to the rest of the plant. The extensive network of roots that penetrates deep in the ground to reach sources of water also stabilizes trees by acting as ballast and an anchor. The majority of roots establish a symbiotic relationship with fungi, forming mycorrhizae. In the mycorrhizae, fungal hyphae grow around the root and within the root around the cells, and in some instances within the cells. This benefits the plant by greatly increasing the surface area for absorption.

Leaves, Sporophylls, and Strobili

A third adaptation marks seedless vascular plants. Accompanying the prominence of the sporophyte and the development of vascular tissue, the appearance of true leaves improved photosynthetic efficiency. Leaves capture more sunlight with their increased surface area.

In addition to photosynthesis, leaves play another role in the life of the plants. Pinecones, mature fronds of ferns, and flowers are all **sporophylls**—leaves that were modified structurally to bear

sporangia. **Strobili** are structures that contain the sporangia. They are prominent in conifers and are known commonly as cones: for example, the pine cones of pine trees.

Lycopodium clavatum is a club moss. (credit: Cory Zanker) Horsetails thrive in a marsh. (credit: Myriam Feldman) Thin leaves originating at the joints are noticeable on the horsetail plant. (credit: Myriam Feldman) Some specimens of this short tree-fern species can grow very tall. (credit: Adrian Pingstone) This chart shows the geological time scale, beginning with the Pre-Archean eon 3800 million years ago and ending with the Quaternary period in present time. (credit: modification of work by USGS) This campus garden was designed by students in the horticulture and landscaping department of the college. (credit: Myriam Feldman)

Seedless Vascular Plants

By the Late Devonian period (385 million years ago), plants had evolved vascular tissue, well-defined leaves, and root systems. With these advantages, plants increased in height and size. During the Carboniferous period (359–299 million years ago), swamp forests of club mosses and horsetails, with some specimens reaching more than 30 meters tall, covered most of the land. These forests gave rise to the extensive coal deposits that gave the Carboniferous its name. In seedless vascular plants, the sporophyte became the

dominant phase of the lifecycle.

Water is still required for fertilization of seedless vascular plants, and most favor a moist environment. Modern-day seedless vascular plants include club mosses, horsetails, ferns, and whisk ferns.

Club Mosses

The **club mosses**, or Lycophyta, are the earliest group of seedless vascular plants. They dominated the landscape of the Carboniferous period, growing into tall trees and forming large swamp forests. Today's club mosses are diminutive, evergreen plants consisting of a stem (which may be branched) and small leaves called microphylls ([link]). The division Lycophyta consists of close to 1,000 species, including quillworts (*Isoetales*), club mosses (Lycopodiales), and spike mosses (Selaginellales): none of which is a true moss.

Horsetails

Ferns and whisk ferns belong to the division Pterophyta. A third group of plants in the Pterophyta, the horsetails, is sometimes classified separately from ferns. **Horsetails** have a single genus, *Equisetum*. They are the survivors of a large group of plants, known as Arthrophyta, which produced large trees and entire swamp forests in the Carboniferous. The plants are usually found in damp environments and marshes ([link]).

The stem of a horsetail is characterized by the presence of joints, or nodes: hence the name Arthrophyta, which means “jointed plant”. Leaves and branches come out as whorls from the evenly spaced rings. The needle-shaped leaves do not contribute greatly to photosynthesis, the majority of which takes place in the green stem ([link]).

Ferns and Whisk Ferns

Ferns are considered the most advanced seedless vascular plants and display characteristics commonly observed in seed plants. Ferns form large leaves and branching roots. In contrast, **whisk ferns**, the psilophytes, lack both roots and leaves, which were probably lost by evolutionary reduction.

Evolutionary reduction is a process by which natural selection reduces the size of a structure that is no longer favorable in a particular environment. Photosynthesis takes place in the green stem of a whisk fern. Small yellow knobs form at the tip of the branch stem and contain the sporangia. Whisk ferns have been classified outside the true ferns; however, recent comparative analysis of DNA suggests that this group may have lost both vascular tissue and roots through evolution, and is actually closely related to ferns.

With their large fronds, **ferns** are the most readily recognizable seedless vascular plants ([link]). About 12,000 species of ferns live in environments ranging from tropics to temperate forests. Although some species survive in dry environments, most ferns are restricted to moist and shaded places. They made their appearance in the fossil record during the Devonian period (416–359 million years ago) and expanded during the Carboniferous period, 359–299 million years ago ([link]).

EON	ERA	PERIOD	MILLIONS OF YEARS AGO
Phanerozoic	Cenozoic	Quaternary	1.6
		Tertiary	66
	Mesozoic	Cretaceous	138
		Jurassic	205
		Triassic	240
	Paleozoic	Permian	290
		Carboniferous	360
		Devonian	410
		Silurian	435
		Ordovician	500
		Cambrian	570
Proterozoic			2500
Archean			3800?
Pre-Archean			

Concept in Action

Watch this video illustrating the life cycle of a fern and assess your knowledge.

Careers in Action

Landscape Designer

Looking at the well-laid gardens of flowers and fountains seen in royal castles and historic houses of Europe, it is clear that the creators of those gardens knew more than art and design. They were also familiar with the biology of the plants they chose. Landscape design also has strong roots in the United States' tradition. A prime example of early American classical design is Monticello, Thomas Jefferson's private estate; among his many other interests, Jefferson maintained a passion for botany. Landscape layout can encompass a small private space, like a backyard garden; public gathering places, like Central Park in New York City; or an entire city plan, like Pierre L'Enfant's design for Washington, DC.

A landscape designer will plan traditional public spaces—such as botanical gardens, parks, college campuses, gardens, and larger developments—as well as natural areas and private gardens ([link]). The restoration of natural places encroached upon by human intervention, such as wetlands, also requires the expertise of a landscape designer. With such an array of required skills, a landscape

designer’s education includes a solid background in botany, soil science, plant pathology, entomology, and horticulture. Coursework in architecture and design software is also required for the completion of the degree. The successful design of a landscape rests on an extensive knowledge of plant growth requirements, such as light and shade, moisture levels, compatibility of different species, and susceptibility to pathogens and pests. For example, mosses and ferns will thrive in a shaded area where fountains provide moisture; cacti, on the other hand, would not fare well in that environment. The future growth of the individual plants must be taken into account to avoid crowding and competition for light and nutrients. The appearance of the space over time is also of concern. Shapes, colors, and biology must be balanced for a well-maintained and sustainable green space. Art, architecture, and biology blend in a beautifully designed and implemented landscape.

Section Summary

Seedless nonvascular plants are small. The dominant stage of the life cycle is the gametophyte. Without a vascular system and roots, they absorb water and nutrients through all of their exposed surfaces. There are three main groups: the liverworts, the hornworts, and the mosses. They are collectively known as bryophytes.

Vascular systems consist of xylem tissue, which transports water and minerals, and phloem tissue, which transports sugars and proteins. With the vascular system, there appeared leaves—large photosynthetic organs—and roots to absorb water

from the ground. The seedless vascular plants include club mosses, which are the most primitive; whisk ferns, which lost leaves and roots by reductive evolution; horsetails, and ferns.

Multiple Choice

Why do mosses grow well in the Arctic tundra?

1. They grow better at cold temperatures.
2. They do not require moisture.
3. They do not have true roots and can grow on hard surfaces.
4. There are no herbivores in the tundra.

C

Which is the most diverse group of seedless vascular plants?

1. the liverworts
2. the horsetails
3. the club mosses
4. the ferns

D

Which group are vascular plants?

1. liverworts
2. mosses
3. hornworts
4. ferns

D

Free Response

What are the three classes of bryophytes?

The bryophytes are divided into three divisions: the liverworts or Marchantiophyta, the hornworts or Anthocerotophyta, and the mosses or true Bryophyta.

How did the development of a vascular system contribute to the increase in size of plants?

It became possible to transport water and nutrients through the plant and not be limited

by rates of diffusion. Vascularization allowed the development of leaves, which increased efficiency of photosynthesis and provided more energy for plant growth.

Glossary

club moss
: the earliest group of seedless vascular plants

fern
: a seedless vascular plant that produces large fronds; the most advanced group of seedless vascular plants

hornwort
: a group of non-vascular plants in which stomata appear

horsetail
: a seedless vascular plant characterized by a jointed stem

liverwort
: the most primitive group of non-vascular plants

moss
: a group of plants in which a primitive conductive system appears

phloem
: the vascular tissue responsible for transport of sugars, proteins, and other solutes

sporophyll
: a leaf modified structurally to bear sporangia

strobili
: cone-like structures that contain the sporangia

whisk fern
: a seedless vascular plant that lost roots and leaves by evolutionary reduction

xylem
: the vascular tissue responsible for long-distance transport of water and nutrients

Seed Plants: Gymnosperms and Angiosperms

By the end of this section, you will be able to:

- Discuss the type of seeds produced by gymnosperms, as well as other characteristics of gymnosperms
- State which period saw the first appearance of gymnosperms and explain when they were the dominant plant life
- List the four groups of modern-day gymnosperms and provide examples of each
- Explain why angiosperms are the dominant form of plant life in most terrestrial ecosystems
- Describe the main parts of a flower and their purpose
- Detail the life cycle of an angiosperm
- Discuss the two main groups of flowering plants

Conifers are the dominant form of vegetation in cold or arid environments and at high altitudes. Shown here are the (a) evergreen spruce *Picea* sp., (b) juniper *Juniperus* sp., (c) sequoia *Sequoia Semervirens*, which is a deciduous gymnosperm, and (d) the tamarack *Larix larcinia*. Notice the yellow leaves of the tamarack. (credit a: modification of work by Rosendahl; credit b: modification of work by Alan Levine; credit c: modification of work by Wendy McCormic; credit d: modification of work by Micky Zlimen) This *Encephalartos ferox* cycad has large cones and broad, fern-like leaves. (credit:

Wendy Cutler) This plate from the 1870 book *Flora Japonica, Sectio Prima (Tafelband)* depicts the leaves and fruit of *Gingko biloba*, as drawn by Philipp Franz von Siebold and Joseph Gerhard Zuccarini.(a) *Ephedra viridis*, known by the common name *Mormon tea*, grows on the West Coast of the United States and Mexico. (b) *Gnetum gnemon* grows in Malaysia. (c) The large *Welwitschia mirabilis* can be found in the Namibian desert. (credit a: modification of work by USDA; credit b: modification of work by Malcolm Manners; credit c: modification of work by Derek Keats)

Gymnosperms: Cone Bearing Plants

Gymnosperms, meaning "naked seeds," are a diverse group of seed plants and are paraphyletic. Paraphyletic groups are those in which not all members are descendants of a single common ancestor. Gymnosperm characteristics include naked seeds, separate female and male gametes, pollination by wind, and a vascular system. Gymnosperm seeds are not enclosed in an ovary; rather, they are exposed on cones or modified leaves.

Gymnosperms were the dominant phylum in Mesozoic era. They are adapted to live where fresh water is scarce during part of the year, or in the nitrogen-poor soil of a bog. Therefore, they are still the prominent phylum in the coniferous biome or

taiga, where the evergreen conifers have a selective advantage in cold and dry weather. Evergreen conifers continue low levels of photosynthesis during the cold months, and are ready to take advantage of the first sunny days of spring. One disadvantage is that conifers are more susceptible than deciduous trees to infestations because conifers do not lose their leaves all at once. They cannot, therefore, shed parasites and restart with a fresh supply of leaves in spring.

The life cycle of a gymnosperm involves alternation of generations, with a dominant sporophyte in which the female gametophyte resides, and reduced gametophytes. The male and female reproductive organs can form in cones. The life cycle of a conifer will serve as our example of reproduction in gymnosperms.

Life Cycle of a Conifer

Pine trees are conifers (cone bearing). The male cones, or staminate cones give rise to pollen grains by meiosis. The pollen grain is the gametophyte and houses two sperm cells. In the spring, large amounts of yellow pollen are released and carried by the wind. Some gametophytes will land on a female cone. Pollination is defined as the initiation of pollen tube growth. The pollen tube grows from the pollen grain slowly, and one of the sperm cells will finally unite with an egg cell in the process of

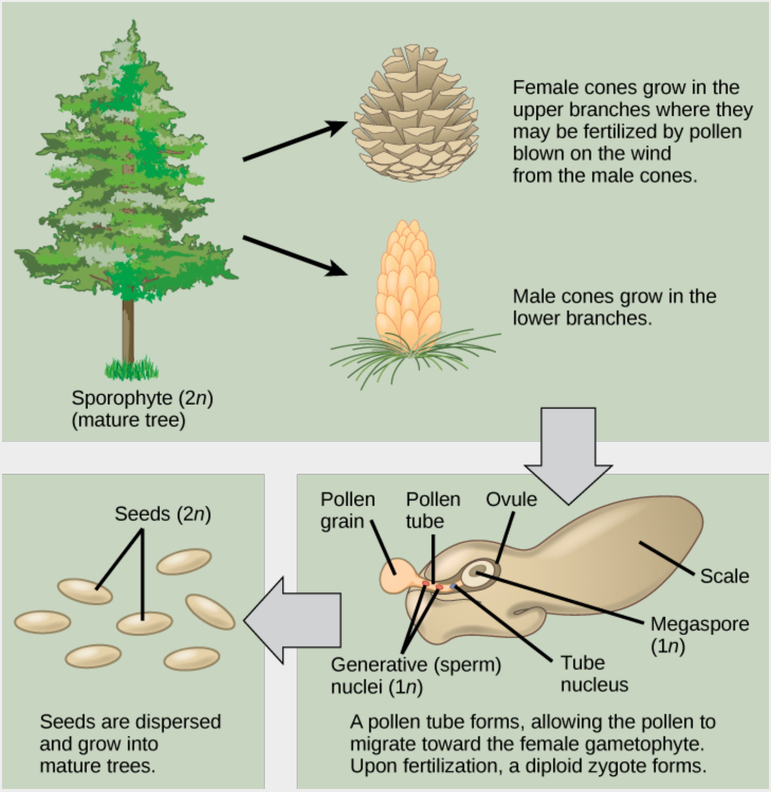
fertilization.

Female cones, or **ovulate cones**, contain two ovules per scale. The ovule is the female gametophyte. Upon fertilization, the diploid egg will give rise to the embryo, which is enclosed in a seed coat of tissue from the parent plant. Fertilization and seed development is a long process in pine trees: it may take up to two years after pollination.

[link] illustrates the life cycle of a conifer. The sporophyte phase is the longest phase in the life of a gymnosperm. The gametophytes are reduced in size.

Art Connection

This image shows the life cycle of a conifer. Pollen from male cones blows up into upper branches, where it fertilizes female cones.



At what stage does the diploid zygote form?

1. when the female cone begins to bud from the tree
2. at fertilization
3. when the seeds drop from the tree
4. when the pollen tube begins to grow

Link to Learning

Watch this video to see the process of seed production in gymnosperms.

Diversity of Gymnosperms

Modern gymnosperms are classified into four phyla. Coniferophyta, Cycadophyta, and Ginkgophyta are similar in their production of secondary cambium (cells that generate the vascular system of the trunk or stem and are partially specialized for water transportation) and their pattern of seed development. However, the three phyla are not closely related phylogenetically to each other. Gnetophyta are considered the closest group to angiosperms because they produce true xylem tissue.

Conifers (Coniferophyta)

Conifers are the dominant phylum of gymnosperms, with the most variety of species ([link]). Most are typically tall trees that usually bear scale-like or needle-like leaves. Water evaporation from leaves is

reduced by their thin shape and the thick cuticle. Snow slides easily off needle-shaped leaves, keeping the load light and decreasing breaking of branches. Adaptations to cold and dry weather explain the predominance of conifers at high altitudes and in cold climates. Conifers include familiar evergreen trees such as pines, spruces, firs, cedars, sequoias, and yews. A few species are deciduous and lose their leaves in fall. The European larch and the tamarack are examples of deciduous conifers ([link]**c**). Many coniferous trees are harvested for paper pulp and timber. The wood of conifers is more primitive than the wood of angiosperms; it contains tracheids, but no vessel elements, and is therefore referred to as “soft wood.”

(a) (b) (c) (d)

Cycads

Cycads thrive in mild climates, and are often mistaken for palms because of the shape of their large, compound leaves. Cycads bear large cones ([link]), and may be pollinated by beetles rather than wind: unusual for a gymnosperm. They dominated the landscape during the age of dinosaurs in the Mesozoic, but only a hundred or so species persisted to modern times. They face possible extinction, and several species are protected through international conventions. Because of their attractive shape, they are often

used as ornamental plants in gardens in the tropics and subtropics.

Gingkophytes

The single surviving species of the **gingkophytes** group is the *Gingko biloba* ([link]). Its fan-shaped leaves—unique among seed plants because they feature a dichotomous venation pattern—turn yellow in autumn and fall from the tree. For centuries, *G. biloba* was cultivated by Chinese Buddhist monks in monasteries, which ensured its preservation. It is planted in public spaces because it is unusually resistant to pollution. Male and female organs are produced on separate plants. Typically, gardeners plant only male trees because the seeds produced by the female plant have an off-putting smell of rancid butter.

Gnetophytes

Gnetophytes are the closest relative to modern angiosperms, and include three dissimilar genera of plants: *Ephedra*, *Gnetum*, and *Welwitschia* ([link]). Like angiosperms, they have broad leaves. In tropical and subtropical zones, gnetophytes are vines or small shrubs. *Ephedra* occurs in dry areas of

the West Coast of the United States and Mexico. *Ephedra*'s small, scale-like leaves are the source of the compound ephedrine, which is used in medicine as a potent decongestant. Because ephedrine is similar to amphetamines, both in chemical structure and neurological effects, its use is restricted to prescription drugs. Like angiosperms, but unlike other gymnosperms, all gnetophytes possess vessel elements in their xylem.

(a) *Ephedra* (b) *Gnetum* (c) *Welwitschia*

Link to Learning

Watch this BBC video describing the amazing strangeness of Welwitschia.

These flowers grow in a botanical garden border in

Bellevue, WA. Flowering plants dominate terrestrial landscapes. The vivid colors of flowers are an adaptation to pollination by animals such as insects and birds. (credit: Myriam Feldman) This image depicts the structure of a perfect flower. Perfect flowers produce both male and female floral organs. The flower shown has only one carpel, but some flowers have a cluster of carpels. Together, all the carpels make up the gynoecium. (credit: modification of work by Mariana Ruiz Villareal) The world's major crops are flowering plants. (a) Rice, (b) wheat, and (c) bananas are monocots, while (d) cabbage, (e) beans, and (f) peaches are dicots. (credit a: modification of work by David Nance, USDA ARS; credit b, c: modification of work by Rosendahl; credit d: modification of work by Bill Tarpenning, USDA; credit e: modification of work by Scott Bauer, USDA ARS; credit f: modification of work by Keith Weller, USDA)

Angiosperms: Flowering Plants

From their humble and still obscure beginning during the early Jurassic period, the angiosperms—or flowering plants—have evolved to dominate most terrestrial ecosystems ([link]). With more than 250,000 species, the angiosperm phylum (Anthophyta) is second only to insects in terms of diversification.

The success of angiosperms is due to two novel reproductive structures: flowers and fruit. The function of the flower is to ensure pollination. Flowers also provide protection for the ovule and developing embryo inside a receptacle. The function of the fruit is seed dispersal. They also protect the developing seed. Different fruit structures or tissues on fruit—such as sweet flesh, wings, parachutes, or spines that grab—reflect the dispersal strategies that help spread seeds.

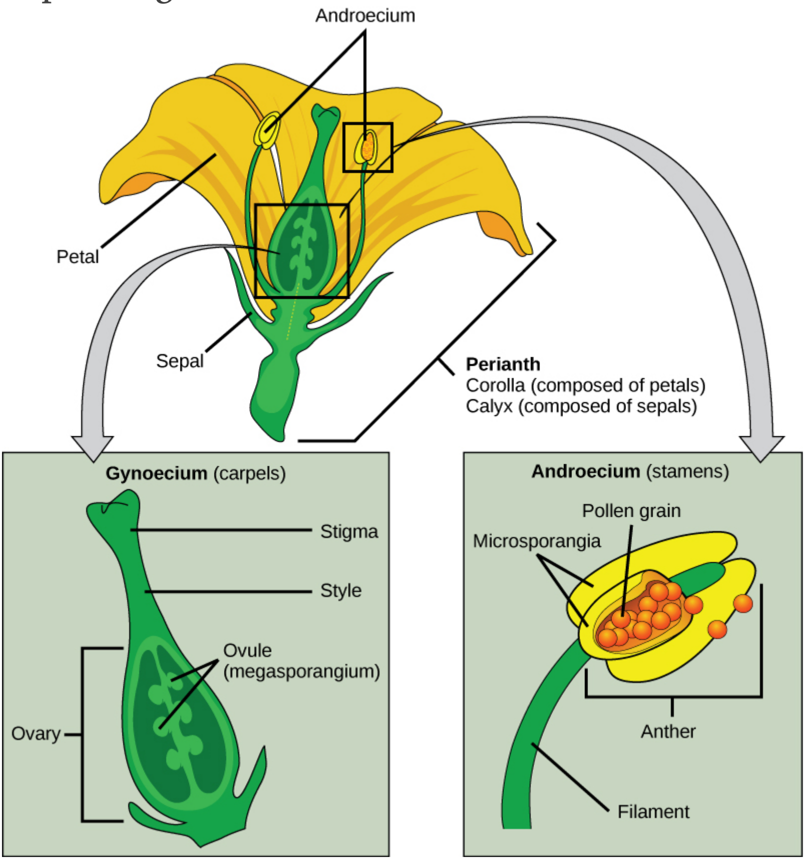
Flowers

Flowers are modified leaves, or sporophylls, organized around a central stalk. Although they vary greatly in appearance, all flowers contain the same structures: sepals, petals, carpels, and stamens.

The peduncle attaches the flower to the plant. A whorl of **sepals** (collectively called the **calyx**) is located at the base of the peduncle and encloses the unopened floral bud. Sepals are usually photosynthetic organs, although there are some exceptions. For example, the corolla in lilies and tulips consists of three sepals and three petals that look virtually identical. **Petals**, collectively the **corolla**, are located inside the whorl of sepals and often display vivid colors to attract pollinators. Flowers pollinated by wind are usually small, feathery, and visually inconspicuous. Sepals and petals together form the **perianth**. The sexual organs (carpels and stamens) are located at the center of the flower.

As illustrated in [link], styles, stigmas, and ovules constitute the female organ: the **gynoecium** or **carpel**. Flower structure is very diverse, and carpels may be singular, multiple, or fused. Multiple fused carpels comprise a **pistil**. The megaspores and the female gametophytes are produced and protected by the thick tissues of the carpel. A long, thin structure called a **style** leads from the sticky **stigma**, where pollen is deposited, to the **ovary**, enclosed in the carpel. The ovary houses one or more ovules, each of which will develop into a seed upon fertilization. The male reproductive organs, the **stamens** (collectively called the androecium), surround the central carpel. Stamens are composed of a thin stalk called a **filament** and a sac-like structure called the

anther. The filament supports the **anther**, where the microspores are produced by meiosis and develop into pollen grains.



Fruit

As the seed develops, the walls of the ovary thicken and form the fruit. The seed forms in an ovary, which also enlarges as the seeds grow. In botany, a fertilized and fully grown, ripened ovary is a fruit. Many foods commonly called vegetables are actually fruit. Eggplants, zucchini, string beans, and bell

peppers are all technically fruit because they contain seeds and are derived from the thick ovary tissue. Acorns are nuts, and winged maple whirligigs (whose botanical name is samara) are also fruit. Botanists classify fruit into more than two dozen different categories, only a few of which are actually fleshy and sweet.

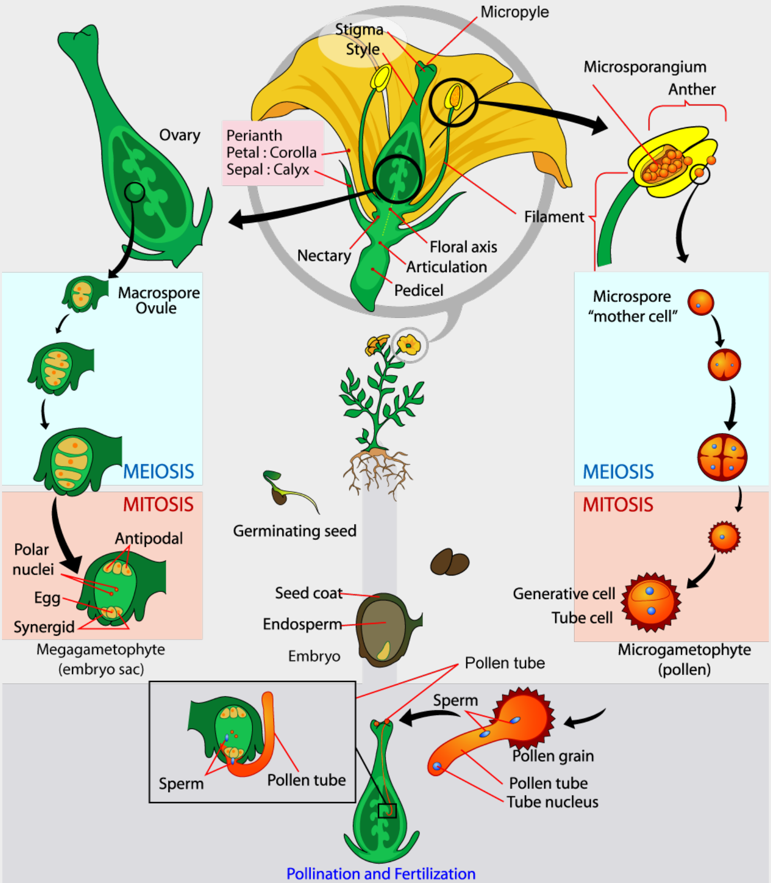
Mature fruit can be fleshy or dry. Fleshy fruit include the familiar berries, peaches, apples, grapes, and tomatoes. Rice, wheat, and nuts are examples of dry fruit. Another distinction is that not all fruits are derived from the ovary. For instance, strawberries are derived from the receptacle and apples from the pericarp, or hypanthium. Some fruits are derived from separate ovaries in a single flower, such as the raspberry. Other fruits, such as the pineapple, form from clusters of flowers. Additionally, some fruits, like watermelon and orange, have rinds. Regardless of how they are formed, fruits are an agent of seed dispersal. The variety of shapes and characteristics reflect the mode of dispersal. Wind carries the light dry fruit of trees and dandelions. Water transports floating coconuts. Some fruits attract herbivores with color or perfume, or as food. Once eaten, tough, undigested seeds are dispersed through the herbivore's feces. Other fruits have burs and hooks to cling to fur and hitch rides on animals.

The Life Cycle of an Angiosperm

The adult, or sporophyte, phase is the main phase of an angiosperm's life cycle ([link]). They generate microspores, which will generate pollen grains as the male gametophytes, and megaspores, which will form an ovule that contains female gametophytes. Inside the anthers' microsporangia, male gametophytes divide by meiosis to generate haploid microspores, which, in turn, undergo mitosis and give rise to pollen grains. Each pollen grain contains two cells: one generative cell that will divide into two sperm and a second cell that will become the pollen tube cell.

Art Connection

The life cycle of an angiosperm is shown. Anthers and carpels are structures that shelter the actual gametophytes: the pollen grain and embryo sac. Double fertilization is a process unique to angiosperms. (credit: modification of work by Mariana Ruiz Villareal)



If a flower lacked a megasporangium, what type of gamete would not form? If the flower lacked a microsporangium, what type of gamete would not form?

A double fertilization event then occurs. One sperm and the egg combine, forming a diploid zygote—the future embryo. The other sperm fuses with the 2*n* polar nuclei, forming a triploid cell that will develop

into the endosperm, which is tissue that serves as a food reserve. The zygote develops into an embryo with a radicle, or small root, and one (monocot) or two (dicot) leaf-like organs called **cotyledons**. This difference in the number of embryonic leaves is the basis for the two major groups of angiosperms: the monocots and the eudicots. Seed food reserves are stored outside the embryo, in the form of complex carbohydrates, lipids or proteins. The cotyledons serve as conduits to transmit the broken-down food reserves from their storage site inside the seed to the developing embryo. The seed consists of a toughened layer of integuments forming the coat, the endosperm with food reserves, and at the center, the well-protected embryo.

Most flowers are monoecious or bisexual, which means that they carry both stamens and carpels; only a few species self-pollinate. Monoecious flowers are also known as “perfect” flowers because they contain both types of sex organs ([link]). Both anatomical and environmental barriers promote cross-pollination mediated by a physical agent (wind or water), or an animal, such as an insect or bird. Cross-pollination increases genetic diversity in a species.

Diversity of Angiosperms

Angiosperms are classified in a single phylum: the **Anthophyta**. Modern angiosperms appear to be a

monophyletic group, which means that they originate from a single ancestor. Flowering plants are divided into two major groups, according to the structure of the cotyledons, pollen grains, and other structures. **Monocots** include grasses and lilies, and eudicots or **dicots** form a polyphyletic group.

Monocots

Plants in the monocot group are primarily identified as such by the presence of a single cotyledon in the seedling. Other anatomical features shared by monocots include veins that run parallel to the length of the leaves, and flower parts that are arranged in a three- or six-fold symmetry. True woody tissue is rarely found in monocots. In palm trees, vascular and parenchyma tissues produced by the primary and secondary thickening meristems form the trunk. The pollen from the first angiosperms was monosulcate, containing a single furrow or pore through the outer layer. This feature is still seen in the modern monocots. Vascular tissue of the stem is not arranged in any particular pattern. The root system is mostly adventitious and unusually positioned, with no major tap root. The monocots include familiar plants such as the true lilies (which are at the origin of their alternate name of Liliopsida), orchids, grasses, and palms. Many important crops are monocots, such as rice and other cereals, corn, sugar cane, and tropical fruits like bananas and pineapples ([link]).

Eudicots

Eudicots, or true dicots, are characterized by the presence of two cotyledons in the developing shoot. Veins form a network in leaves, and flower parts come in four, five, or many whorls. Vascular tissue forms a ring in the stem; in monocots, vascular tissue is scattered in the stem. Eudicots can be **herbaceous** (like grasses), or produce woody tissues. Most eudicots produce pollen that is trisulcate or triporate, with three furrows or pores. The root system is usually anchored by one main root developed from the embryonic radicle. Eudicots comprise two-thirds of all flowering plants. The major differences between monocots and eudicots are summarized in [link]. Many species exhibit characteristics that belong to either group; as such, the classification of a plant as a monocot or a

eudicot is not always clearly evident.

Comparison of Structural Characteristics of Monocots and Eudicots

Characteristic	Monocot	Eudicot
Cotyledon	One	Two
Veins in Leaves	Parallel	Network (branched)
Stem Vascular Tissue	Scattered	Arranged in ring pattern
Roots	Network of adventitious roots	Tap root with many lateral roots
Pollen	Monosulcate	Trisulcate
Flower Parts	Three or multiple of three	Four, five, multiple of four or five and whorls

Section Summary

Gymnosperms are seed plants that produce naked seeds. They appeared in the Paleozoic period and were the dominant plant life during the Mesozoic. Modern-day gymnosperms belong to four phyla. The largest phylum, Coniferophyta, is represented by conifers, the predominant plants at high altitude and latitude. Cycads (phylum Cycadophyta) resemble palm trees and grow in tropical climates. *Gingko biloba* is the only representative of the phylum Gingkophyta. The last phylum, Gnetophyta, is a diverse group of shrubs that produce vessel elements in their wood.

Angiosperms are the dominant form of plant life in most terrestrial ecosystems, comprising about 90 percent of all plant species. Most crops and ornamental plants are angiosperms. Their success comes from two innovative structures that protect reproduction from variability in the environment: the flower and the fruit. Flowers were derived from modified leaves. The main parts of a flower are the sepals and petals, which protect the reproductive parts: the stamens and the carpels. The stamens produce the male gametes in pollen grains. The carpels contain the female gametes (the eggs inside the ovules), which are within the ovary of a carpel. The walls of the ovary thicken after fertilization, ripening into fruit that ensures dispersal by wind, water, or animals.

The angiosperm life cycle is dominated by the

sporophyte stage. Double fertilization is an event unique to angiosperms. One sperm in the pollen fertilizes the egg, forming a diploid zygote, while the other combines with the two polar nuclei, forming a triploid cell that develops into a food storage tissue called the endosperm. Flowering plants are divided into two main groups, the monocots and eudicots, according to the number of cotyledons in the seedlings. Basal angiosperms belong to an older lineage than monocots and eudicots.

Art Connections

[link] At what stage does the diploid zygote form?

1. When the female cone begins to bud from the tree
2. At fertilization
3. When the seeds drop from the tree
4. When the pollen tube begins to grow

[link] B. The diploid zygote forms after the pollen tube has finished forming, so that the male generative nuclei can fuse with the female gametophyte.

[link] If a flower lacked a megasporangium, what type of gamete would not form? If the flower lacked a microsporangium, what type of gamete would not form?

[link] Without a megasporangium, an egg would not form; without a microsporangium, pollen would not form.

Review Questions

Which of the following traits characterizes gymnosperms?

1. The plants carry exposed seeds on modified leaves.
2. Reproductive structures are located in a flower.
3. After fertilization, the ovary thickens and forms a fruit.
4. The gametophyte is longest phase of the life cycle.

A

In the northern forests of Siberia, a tall tree is most likely a:

1. conifer
2. cycad
3. *Gingko biloba*
4. gnetophyte

A

Which of the following structures in a flower is not directly involved in reproduction?

1. the style
2. the stamen
3. the sepal
4. the anther

C

Pollen grains develop in which structure?

1. the anther
2. the stigma
3. the filament
4. the carpel

A

In the course of double fertilization, one sperm cell fuses with the egg and the second one fuses with ______.

1. the synergids
2. the polar nuclei of the center cell
3. the egg as well
4. the antipodal cells

B

Corn develops from a seedling with a single cotyledon, displays parallel veins on its leaves, and produces monosulcate pollen. It is most likely:

1. a gymnosperm
2. a monocot
3. a eudicot
4. a basal angiosperm

B

Free Response

The Mediterranean landscape along the sea shore is dotted with pines and cypresses. The weather is not cold, and the trees grow at sea level. What evolutionary adaptation of conifers makes them suitable to the Mediterranean climate?

The trees are adapted to arid weather, and do not lose as much water due to transpiration as non-conifers.

What are the four modern-day phyla of gymnosperms?

The four modern-day phyla of gymnosperms are Coniferophyta, Cycadophyta, Gingkophyta, and Gnetophyta.

Some cycads are considered endangered species and their trade is severely restricted. Customs officials stop suspected smugglers who claim that the plants in their possession are palm trees, not cycads. How would a botanist distinguish between the two types of plants?

The resemblance between cycads and palm

trees is only superficial. Cycads are gymnosperms and do not bear flowers or fruit. Cycads produce cones: large, female cones that produce naked seeds, and smaller male cones on separate plants. Palms do not.

What are the two structures that allow angiosperms to be the dominant form of plant life in most terrestrial ecosystems?

Angiosperms are successful because of flowers and fruit. These structures protect reproduction from variability in the environment.

Glossary

anther
: sac-like structure at the tip of the stamen in which pollen grains are produced

Anthophyta
: phylum to which angiosperms belong

basal angiosperms
: a group of plants that probably branched off before the separation of monocots and eudicots

calyx

whorl of sepals

carpel
: single unit of the pistil

conifer
: dominant phylum of gymnosperms with the most variety of trees

cycad
: gymnosperm that grows in tropical climates and resembles a palm tree; member of the phylum Cycadophyta

corolla
: collection of petals

cotyledon
: primitive leaf that develop in the zygote; monocots have one cotyledon, and dicots have two cotyledons

dicot
: (also, eudicot) related group of angiosperms whose embryos possess two cotyledons

filament
: thin stalk that links the anther to the base of the flower

gingkophyte
: gymnosperm with one extant species, the *Gingko biloba*: a tree with fan-shaped leaves

gnetophyte
: gymnosperm shrub with varied morphological features that produces vessel elements in its woody tissues; the phylum includes the genera *Ephedra, Gnetum* and *Welwitschia*

gymnosperm
: seed plant with naked seeds (seeds exposed on modified leaves or in cones)

gynoecium
: (also, carpel) structure that constitute the female reproductive organ

herbaceous
: grass-like plant noticeable by the absence of woody tissue

monocot
: related group of angiosperms that produce embryos with one cotyledon and pollen with a single ridge

ovary
: chamber that contains and protects the ovule or female megasporangium

ovulate cone
: cone containing two ovules per scale

perianth
: part of the plant consisting of the calyx

(sepals) and corolla (petals)

petal
: modified leaf interior to the sepals; colorful petals attract animal pollinators

pistil
: fused group of carpels

sepal
: modified leaf that encloses the bud; outermost structure of a flower

stamen
: structure that contains the male reproductive organs

stigma
: uppermost structure of the carpel where pollen is deposited

style
: long, thin structure that links the stigma to the ovary

Characteristics of Fungi

By the end of this section, you will be able to:

- List the characteristics of fungi
- Describe the composition of the mycelium
- Describe the mode of nutrition of fungi
- Explain sexual and asexual reproduction in fungi

Although humans have used yeasts and mushrooms since prehistoric times, until recently, the biology of fungi was poorly understood. Up until the mid-20th century, many scientists classified fungi as plants. Fungi, like plants, arose mostly sessile and seemingly rooted in place. They possess a stem-like structure similar to plants, as well as having a root-like fungal mycelium in the soil. In addition, their mode of nutrition was poorly understood. Progress in the field of fungal biology was the result of **mycology**: the scientific study of fungi. Based on fossil evidence, fungi appeared in the pre-Cambrian era, about 450 million years ago. Molecular biology analysis of the fungal genome demonstrates that fungi are more closely related to animals than plants. They are a polyphyletic group of organisms that share characteristics, rather than sharing a single common ancestor.

Career Connection

Mycologist

Mycologists are biologists who study fungi. Mycology is a branch of microbiology, and many mycologists start their careers with a degree in microbiology. To become a mycologist, a bachelor's degree in a biological science (preferably majoring in microbiology) and a master's degree in mycology are minimally necessary. Mycologists can specialize in taxonomy and fungal genomics, molecular and cellular biology, plant pathology, biotechnology, or biochemistry. Some medical microbiologists concentrate on the study of infectious diseases caused by fungi (mycoses). Mycologists collaborate with zoologists and plant pathologists to identify and control difficult fungal infections, such as the devastating chestnut blight, the mysterious decline in frog populations in many areas of the world, or the deadly epidemic called white nose syndrome, which is decimating bats in the Eastern United States.

Government agencies hire mycologists as research scientists and technicians to monitor the health of crops, national parks, and national forests. Mycologists are also employed in the private sector by companies that develop chemical and biological control products or new agricultural products, and by companies that provide disease control services. Because of the key role played by fungi in the fermentation of alcohol and the preparation of many important foods, scientists with a good understanding of fungal physiology routinely work

in the food technology industry. Oenology, the science of wine making, relies not only on the knowledge of grape varietals and soil composition, but also on a solid understanding of the characteristics of the wild yeasts that thrive in different wine-making regions. It is possible to purchase yeast strains isolated from specific grape-growing regions. The great French chemist and microbiologist, Louis Pasteur, made many of his essential discoveries working on the humble brewer's yeast, thus discovering the process of fermentation.

The poisonous *Amanita muscaria* is native to temperate and boreal regions of North America. (credit: Christine Majul) *Candida albicans* is a yeast cell and the agent of candidiasis and thrush. This organism has a similar morphology to coccus bacteria; however, yeast is a eukaryotic organism (note the nucleus). (credit: modification of work by Dr. Godon Roberstad, CDC; scale-bar data from Matt Russell) The mycelium of the fungus *Neotestudina rosati* can be pathogenic to humans. The fungus enters through a cut or scrape and develops a mycetoma, a chronic subcutaneous infection. (credit: CDC) Fungal hyphae may be (a) septated or (b) coenocytic (coeno- = "common"; -cytic = "cell") with many nuclei present in a single hypha. A bright field light micrograph of (c) *Phialophora richardsiae*

shows septa that divide the hyphae. (credit c: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

Cell Structure and Function

Fungi are eukaryotes, and as such, have a complex cellular organization. As eukaryotes, fungal cells contain a membrane-bound nucleus. The DNA in the nucleus is wrapped around histone proteins, as is observed in other eukaryotic cells. A few types of fungi have structures comparable to bacterial plasmids (loops of DNA); however, the horizontal transfer of genetic information from one mature bacterium to another rarely occurs in fungi. Fungal cells also contain mitochondria and a complex system of internal membranes, including the endoplasmic reticulum and Golgi apparatus.

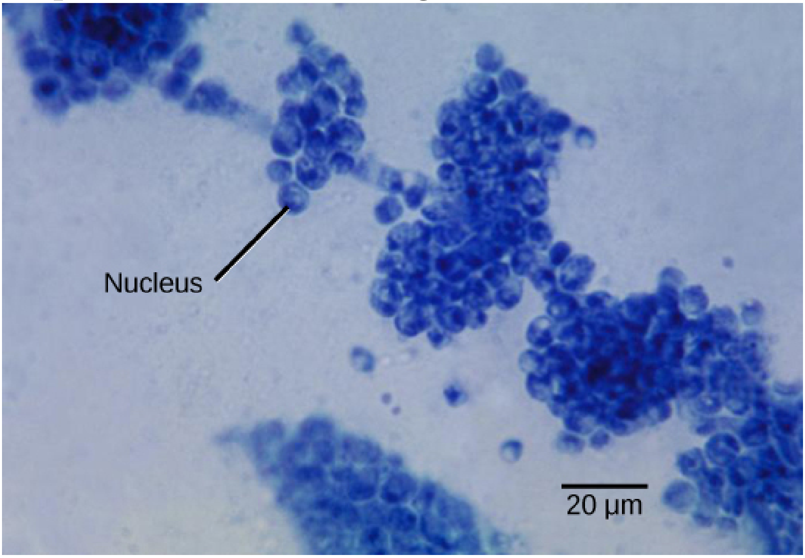
Unlike plant cells, fungal cells do not have chloroplasts or chlorophyll. Many fungi display bright colors arising from other cellular pigments, ranging from red to green to black. The poisonous *Amanita muscaria* (fly agaric) is recognizable by its bright red cap with white patches ([link]). Pigments in fungi are associated with the cell wall and play a protective role against ultraviolet radiation. Some fungal pigments are toxic.

Like plant cells, fungal cells have a thick cell wall. The rigid layers of fungal cell walls contain complex polysaccharides called chitin and glucans. Chitin, also found in the exoskeleton of insects, gives structural strength to the cell walls of fungi. The wall protects the cell from desiccation and predators. Fungi have plasma membranes similar to other eukaryotes, except that the structure is stabilized by ergosterol: a steroid molecule that replaces the cholesterol found in animal cell membranes. Most members of the kingdom Fungi are nonmotile. Flagella are produced only by the gametes in the primitive Phylum Chytridiomycota.

Growth

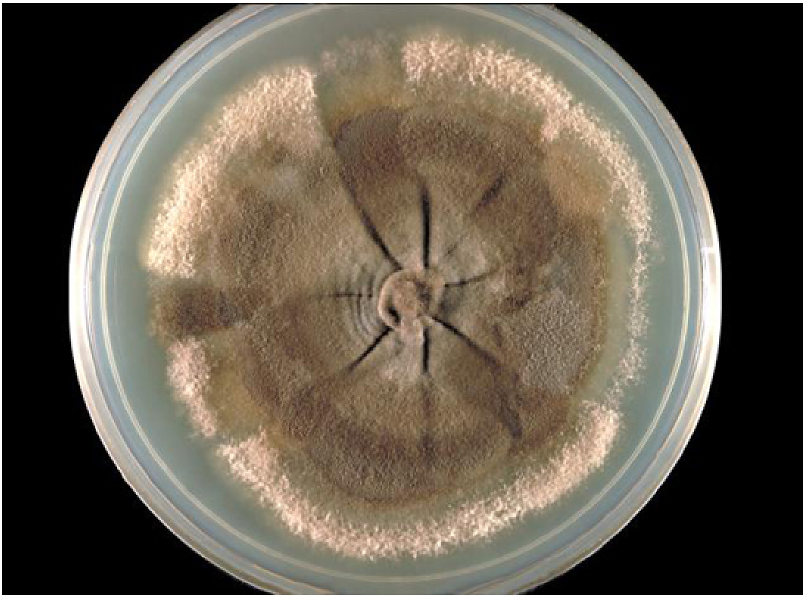
The vegetative body of a fungus is a unicellular or multicellular **thallus**. Dimorphic fungi can change

from the unicellular to multicellular state depending on environmental conditions. Unicellular fungi are generally referred to as **yeasts**. *Saccharomyces cerevisiae* (baker's yeast) and *Candida* species (the agents of thrush, a common fungal infection) are examples of unicellular fungi ([link]).

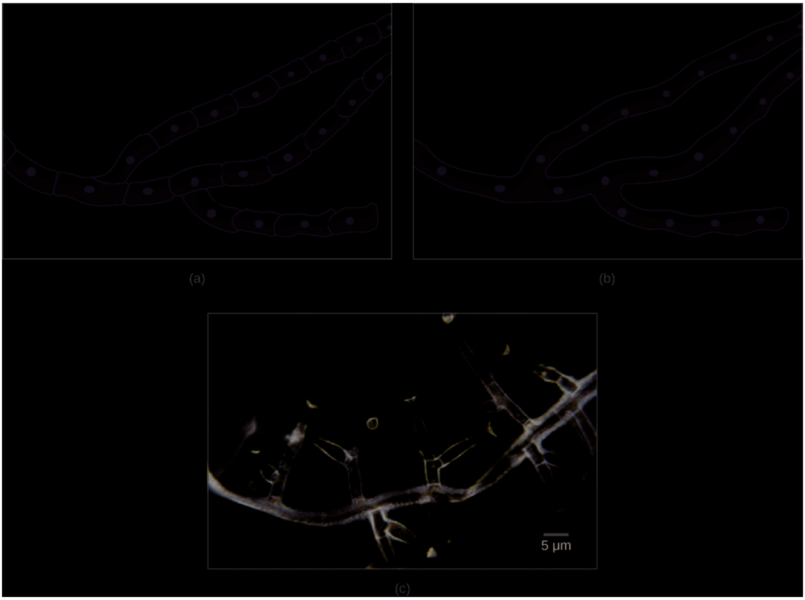


Most fungi are multicellular organisms. They display two distinct morphological stages: the vegetative and reproductive. The vegetative stage consists of a tangle of slender thread-like structures called **hyphae** (singular, **hypha**), whereas the reproductive stage can be more conspicuous. The mass of hyphae is a **mycelium** ([link]). It can grow on a surface, in soil or decaying material, in a liquid, or even on living tissue. Although individual hyphae must be observed under a microscope, the mycelium of a fungus can be very large, with some species truly being "the fungus humongous." The

giant *Armillaria solidipes* (honey mushroom) is considered the largest organism on Earth, spreading across more than 2,000 acres of underground soil in eastern Oregon; it is estimated to be at least 2,400 years old.



Most fungal hyphae are divided into separate cells by endwalls called **septa** (singular, **septum**) ([link]**a, c**). In most phyla of fungi, tiny holes in the septa allow for the rapid flow of nutrients and small molecules from cell to cell along the hypha. They are described as perforated septa. The hyphae in bread molds (which belong to the Phylum Zygomycota) are not separated by septa. Instead, they are formed by large cells containing many nuclei, an arrangement described as **coenocytic hyphae** ([link]**b**).



Fungi thrive in environments that are moist and slightly acidic, and can grow with or without light. They vary in their oxygen requirement. Most fungi are **obligate aerobes**, requiring oxygen to survive. Other species, such as the Chytridiomycota that reside in the rumen of cattle, are are **obligate anaerobes**, in that they only use anaerobic respiration because oxygen will disrupt their metabolism or kill them. Yeasts are intermediate, being **faculative anaerobes**. This means that they grow best in the presence of oxygen using aerobic respiration, but can survive using anaerobic respiration when oxygen is not available. The alcohol produced from yeast fermentation is used in wine and beer production.

Nutrition

Like animals, fungi are heterotrophs; they use complex organic compounds as a source of carbon, rather than fix carbon dioxide from the atmosphere as do some bacteria and most plants. In addition, fungi do not fix nitrogen from the atmosphere. Like animals, they must obtain it from their diet. However, unlike most animals, which ingest food and then digest it internally in specialized organs, fungi perform these steps in the reverse order; digestion precedes ingestion. First, exoenzymes are transported out of the hyphae, where they process nutrients in the environment. Then, the smaller molecules produced by this external digestion are absorbed through the large surface area of the mycelium. As with animal cells, the polysaccharide of storage is glycogen, rather than starch, as found in plants.

Fungi are mostly **saprobes** (saprophyte is an equivalent term): organisms that derive nutrients from decaying organic matter. They obtain their nutrients from dead or decomposing organic matter: mainly plant material. Fungal exoenzymes are able to break down insoluble polysaccharides, such as the cellulose and lignin of dead wood, into readily absorbable glucose molecules. The carbon, nitrogen, and other elements are thus released into the environment. Because of their varied metabolic pathways, fungi fulfill an important ecological role and are being investigated as potential tools in bioremediation. For example, some species of fungi

can be used to break down diesel oil and polycyclic aromatic hydrocarbons (PAHs). Other species take up heavy metals, such as cadmium and lead.

Some fungi are parasitic, infecting either plants or animals. Smut and Dutch elm disease affect plants, whereas athlete's foot and candidiasis (thrush) are medically important fungal infections in humans. In environments poor in nitrogen, some fungi resort to predation of nematodes (small non-segmented roundworms). Species of *Arthrobotrys* fungi have a number of mechanisms to trap nematodes. One mechanism involves constricting rings within the network of hyphae. The rings swell when they touch the nematode, gripping it in a tight hold. The fungus penetrates the tissue of the worm by extending specialized hyphae called **haustoria**. Many parasitic fungi possess haustoria, as these structures penetrate the tissues of the host, release digestive enzymes within the host's body, and absorb the digested nutrients.

The (a) giant puff ball mushroom releases (b) a cloud of spores when it reaches maturity. (credit a: modification of work by Roger Griffith; credit b: modification of work by Pearson Scott Foresman, donated to the Wikimedia Foundation) The dark cells in this bright field light micrograph are the pathogenic yeast *Histoplasma capsulatum,* seen against a backdrop of light blue tissue. Histoplasma primarily infects lungs but can spread to other tissues, causing histoplasmosis, a potentially fatal

disease. (credit: modification of work by Dr. Libero Ajello, CDC; scale-bar data from Matt Russell) Fungi may have both asexual and sexual stages of reproduction. This bright field light micrograph shows the release of spores from a sporangium at the end of a hypha called a sporangiophore. The organism is a *Mucor* sp. fungus, a mold often found indoors. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

Reproduction

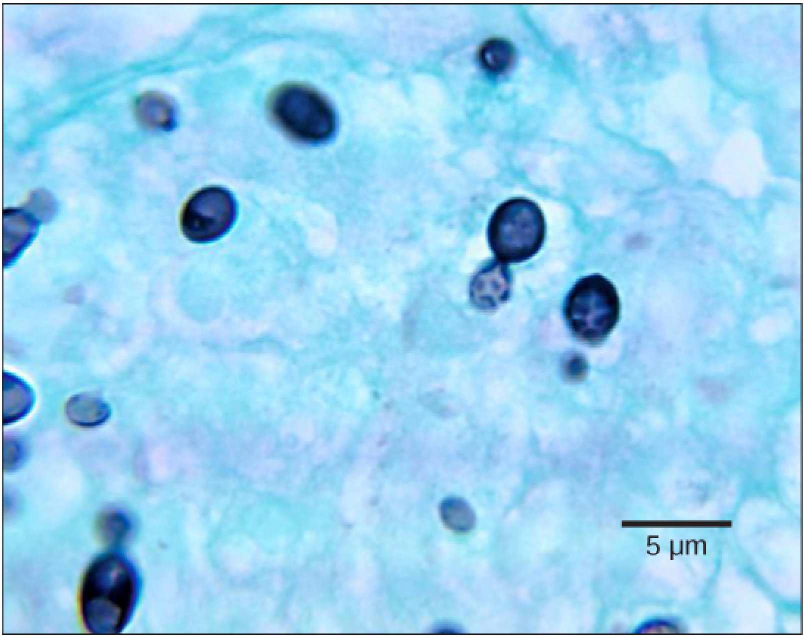
Fungi reproduce sexually and/or asexually. Perfect fungi reproduce both sexually and asexually, while the so-called imperfect fungi reproduce only asexually (by mitosis).

In both sexual and asexual reproduction, fungi produce spores that disperse from the parent organism by either floating on the wind or hitching a ride on an animal. Fungal spores are smaller and lighter than plant seeds. The giant puffball mushroom bursts open and releases trillions of spores. The huge number of spores released increases the likelihood of landing in an environment that will support growth ([link]).

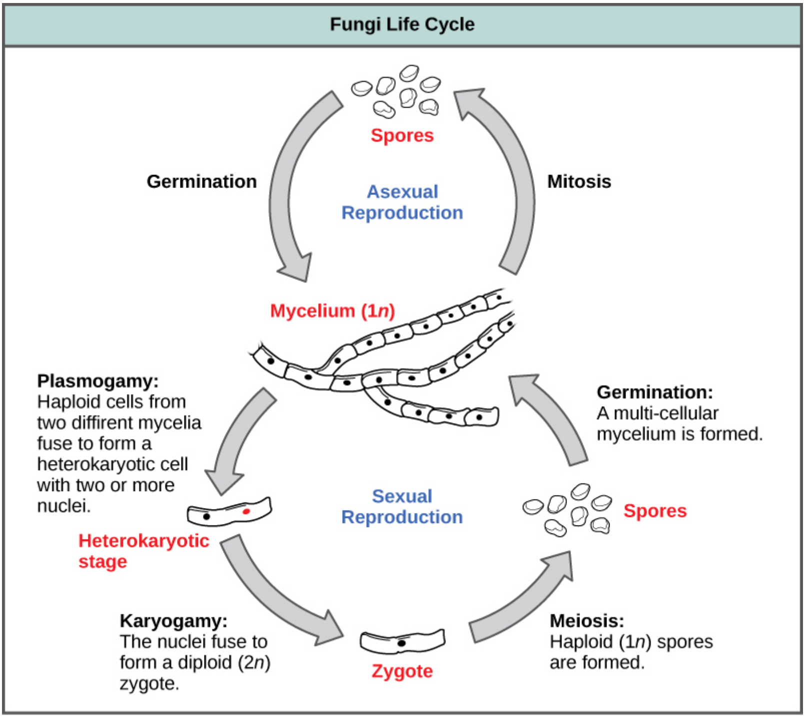
(a) (b)

Asexual Reproduction

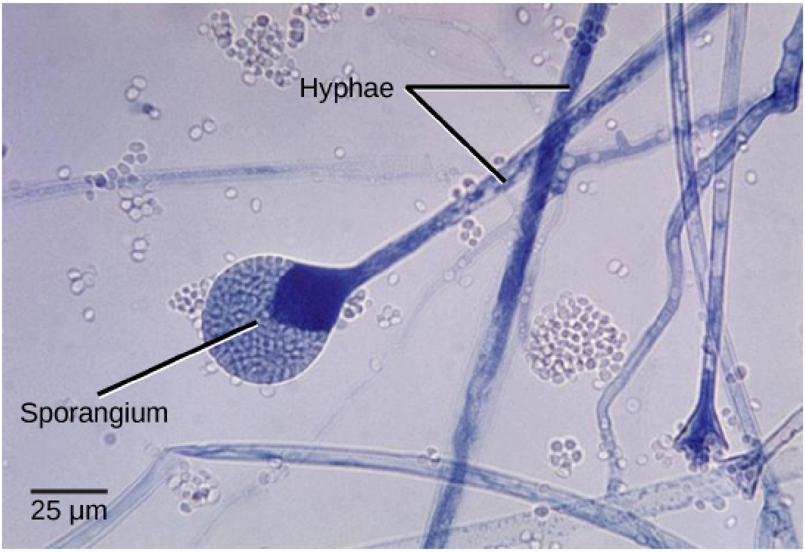
Fungi reproduce asexually by fragmentation, budding, or producing spores. Fragments of hyphae can grow new colonies. Somatic cells in yeast form buds. During budding (a type of cytokinesis), a bulge forms on the side of the cell, the nucleus divides mitotically, and the bud ultimately detaches itself from the mother cell ([link]).



The most common mode of asexual reproduction is through the formation of asexual spores, which are produced by one parent only (through mitosis) and are genetically identical to that parent ([link]). Spores allow fungi to expand their distribution and colonize new environments. They may be released from the parent thallus either outside or within a special reproductive sac called a **sporangium**.



There are many types of asexual spores. Conidiospores are unicellular or multicellular spores that are released directly from the tip or side of the hypha. Other asexual spores originate in the fragmentation of a hypha to form single cells that are released as spores; some of these have a thick wall surrounding the fragment. Yet others bud off the vegetative parent cell. Sporangiospores are produced in a sporangium ([link]).



Sexual Reproduction

Sexual reproduction introduces genetic variation into a population of fungi. In fungi, sexual reproduction often occurs in response to adverse environmental conditions. During sexual reproduction, two mating types are produced. When both mating types are present in the same mycelium, it is called **homothallic**, or self-fertile. **Heterothallic** mycelia require two different, but compatible, mycelia to reproduce sexually.

Although there are many variations in fungal sexual reproduction, all include the following three stages ([link]). First, during **plasmogamy** (literally, “marriage or union of cytoplasm”), two haploid cells fuse, leading to a dikaryotic stage where two haploid nuclei coexist in a single cell. During

karyogamy ("nuclear marriage"), the haploid nuclei fuse to form a diploid zygote nucleus. Finally, meiosis takes place in the gametangia (singular, gametangium) organs, in which gametes of different mating types are generated. At this stage, spores are disseminated into the environment.

Link to Learning

Review the characteristics of fungi by visiting this interactive site from Wisconsin-online.

Section Summary

Fungi are eukaryotic organisms that appeared on land more than 450 million years ago. They are heterotrophs and contain neither photosynthetic

pigments such as chlorophyll, nor organelles such as chloroplasts. Because fungi feed on decaying and dead matter, they are saprobes. Fungi are important decomposers that release essential elements into the environment. External enzymes digest nutrients that are absorbed by the body of the fungus, which is called a thallus. A thick cell wall made of chitin surrounds the cell. Fungi can be unicellular as yeasts, or develop a network of filaments called a mycelium, which is often described as mold. Most species multiply by asexual and sexual reproductive cycles and display an alternation of generations. Another group of fungi do not have a sexual cycle. Sexual reproduction involves plasmogamy (the fusion of the cytoplasm), followed by karyogamy (the fusion of nuclei). Meiosis regenerates haploid individuals, resulting in haploid spores.

Review Questions

Which polysaccharide is usually found in the cell wall of fungi?

1. starch
2. glycogen
3. chitin
4. cellulose

C

Which of these organelles is not found in a fungal cell?

1. chloroplast
2. nucleus
3. mitochondrion
4. Golgi apparatus

A

The wall dividing individual cells in a fungal filament is called a

1. thallus
2. hypha
3. mycelium
4. septum

D

During sexual reproduction, a homothallic mycelium contains

1. all septated hyphae
2. all haploid nuclei

3. both mating types
4. none of the above

C

Free Response

What are the evolutionary advantages for an organism to reproduce both asexually and sexually?

Asexual reproduction is fast and best under favorable conditions. Sexual reproduction allows the recombination of genetic traits and increases the odds of developing new adaptations better suited to a changed environment.

Compare plants, animals, and fungi, considering these components: cell wall, chloroplasts, plasma membrane, food source, and polysaccharide storage. Be sure to indicate fungi's similarities and differences to plants and animals.

Animals have no cell walls; fungi have cell walls containing chitin; plants have cell walls containing cellulose. Chloroplasts are absent in both animals and fungi but are present in plants. Animal plasma membranes are stabilized with cholesterol, while fungi plasma membranes are stabilized with ergosterol, and plant plasma membranes are stabilized with phytosterols. Animals obtain N and C from food sources via internal digestion. Fungi obtain N and C from food sources via external digestion. Plants obtain organic N from the environment or through symbiotic N-fixing bacteria; they obtain C from photosynthesis. Animals and fungi store polysaccharides as glycogen, while plants store them as starch.

Glossary

coenocytic hypha
: single hypha that lacks septa and contains many nuclei

faculative anaerobes
: organisms that can perform both aerobic and anaerobic respiration and can survive in oxygen-rich and oxygen-poor environment

haustoria
: modified hyphae on many parasitic fungi that penetrate the tissues of their hosts, release

digestive enzymes, and/or absorb nutrients from the host

heterothallic
: describes when only one mating type is present in an individual mycelium

homothallic
: describes when both mating types are present in mycelium

hypha
: fungal filament composed of one or more cells

karyogamy
: fusion of nuclei

mycelium
: mass of fungal hyphae

mycology
: scientific study of fungi

obligate aerobes
: organisms, such as humans, that must perform aerobic respiration to survive

obligate anaerobes
: organisms that only perform anaerobic respiration and often cannot survive in the presence of oxygen

plasmogamy

fusion of cytoplasm

saprobe
organism that derives nutrients from decaying organic matter; also saprophyte

septa
cell wall division between hyphae

sporangium
reproductive sac that contains spores

thallus
vegetative body of a fungus

yeast
general term used to describe unicellular fungi

Classifications of Fungi

By the end of this section, you will be able to do the following:

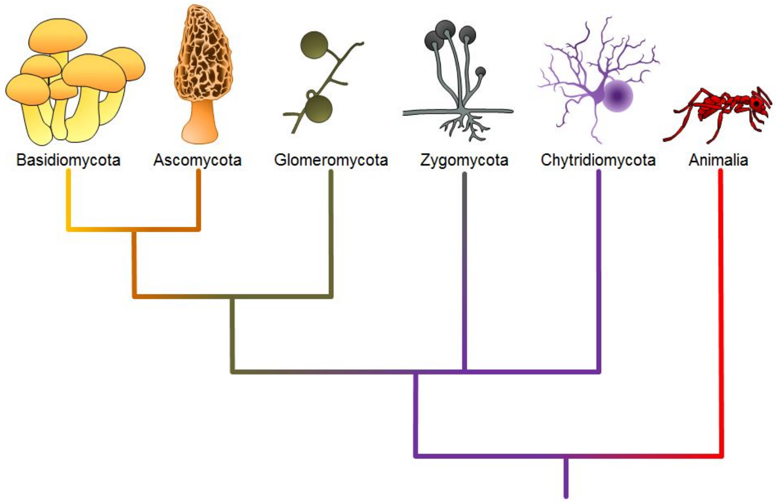
- Identify fungi and place them into the five major phyla according to current classification
- Describe each phylum in terms of major representative species and patterns of reproduction

The kingdom Fungi contains five major phyla that were established according to their mode of sexual reproduction or using molecular data. Polyphyletic, unrelated fungi that reproduce without a sexual cycle, were once placed for convenience in a sixth group, the Deuteromycota, called a "form phylum," because superficially they appeared to be similar. However, most mycologists have discontinued this practice. Rapid advances in molecular biology and the sequencing of 18S rRNA (ribosomal RNA) continue to show new and different relationships among the various categories of fungi.

The five true phyla of fungi are the Chytridiomycota (Chytrids), the Zygomycota (conjugated fungi), the Ascomycota (sac fungi), the Basidiomycota (club fungi) and the recently described Phylum Glomeromycota ([link]).

Fungal phyla. Note: "-mycota" is used to designate a phylum while "-mycetes" formally denotes a class or is used informally to refer to all members of the

phylum.



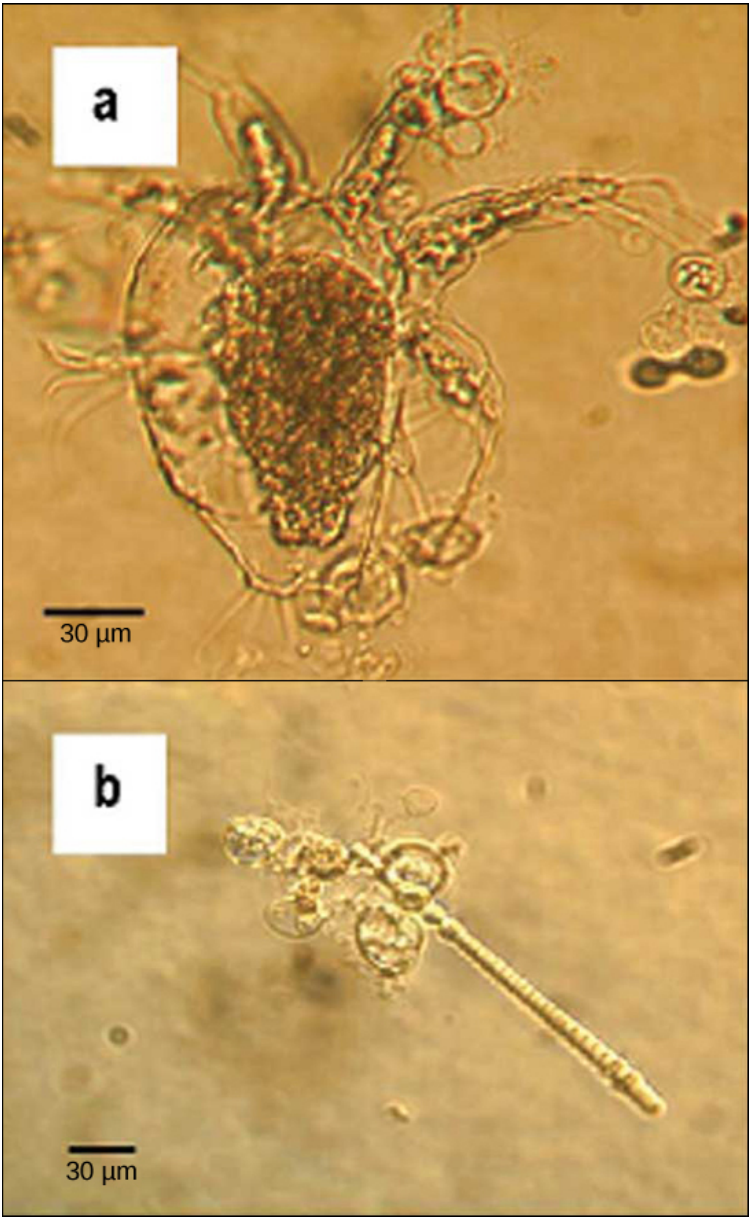
Chytrids. The chytrid *Batrachochytrium dendrobatidis* is seen in these light micrographs as transparent spheres growing on (a) a freshwater arthropod (water mite) and (b) algae. This chytrid causes skin diseases in many species of amphibians, resulting in species decline and extinction. (credit: modification of work by Johnson ML, Speare R., CDC)

Chytridiomycota: The Chytrids

The only class in the Phylum Chytridiomycota is the **Chytridiomycetes**. The chytrids are the simplest and most primitive Eumycota, or true fungi. The evolutionary record shows that the first recognizable chytrids appeared during the late pre-Cambrian period, more than 500 million years ago. Like all fungi, chytrids have chitin in their cell walls, but one group of chytrids has both cellulose

and chitin in the cell wall. Most chytrids are unicellular; however, a few form multicellular organisms and hyphae, which have no septa between cells (coenocytic). The Chytrids are the only fungi that have retained flagella. They produce both gametes and diploid zoospores that swim with the help of a single flagellum. An unusual feature of the chytrids is that both male and female gametes are flagellated.

The ecological habitat and cell structure of chytrids have much in common with protists. Chytrids usually live in aquatic environments, although some species live on land. Some species thrive as parasites on plants, insects, or amphibians ([link]), while others are saprobes. The chytrid species *Allomyces* is well characterized as an experimental organism. Its reproductive cycle includes both asexual and sexual phases. *Allomyces* produces diploid or haploid flagellated zoospores in a sporangium.



Zygomycete life cycle. Zygomycetes have asexual and sexual phases in their life cycles. In the asexual phase, spores are produced from haploid sporangia by mitosis (not shown). In the sexual phase, plus

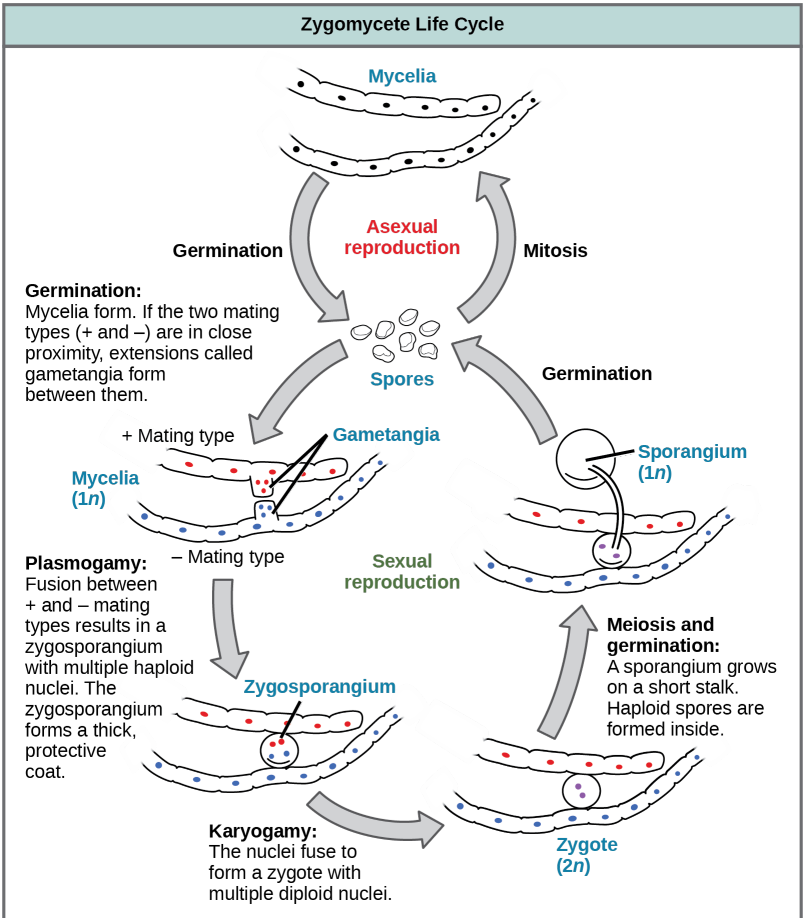
and minus haploid mating types conjugate to form a heterokaryotic zygosporangium. Karyogamy then produces a diploid zygote. Diploid cells in the zygote undergo meiosis and germinate to form a haploid sporangium, which releases the next generation of haploid spores. Rhizopus spores. Asexual sporangia grow at the end of stalks, which appear as (a) white fuzz seen on this bread mold, *Rhizopus stolonifer*. The black tips (b) of bread mold are the spore-containing sporangia. (credit b: modification of work by "polandeze"/Flickr)

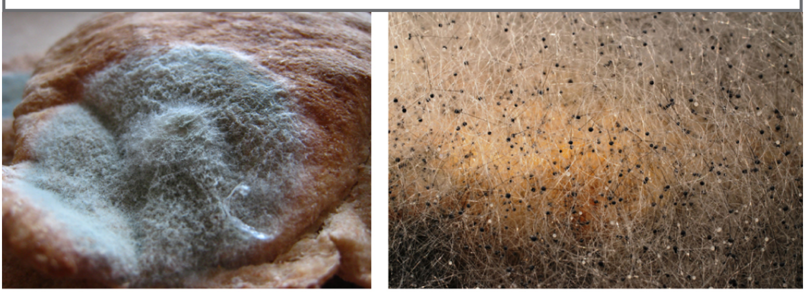
Zygomycota: The Conjugated Fungi

The zygomycetes are a relatively small group of fungi belonging to the Phylum **Zygomycota**. They include the familiar bread mold, *Rhizopus stolonifer*, which rapidly propagates on the surfaces of breads, fruits, and vegetables. Most species are saprobes, living off decaying organic material; a few are parasites, particularly of insects. Zygomycetes play a considerable commercial role. For example, the metabolic products of some species of *Rhizopus* are intermediates in the synthesis of semi-synthetic steroid hormones.

Zygomycetes have a thallus of coenocytic hyphae in which the nuclei are haploid when the organism is in the vegetative stage. The fungi usually reproduce asexually by producing sporangiospores ([link]). The black tips of bread mold are the swollen

sporangia packed with black spores ([link]). When spores land on a suitable substrate, they germinate and produce a new mycelium. Sexual reproduction starts when environmental conditions become unfavorable. Two opposing mating strains (type + and type –) must be in close proximity for gametangia from the hyphae to be produced and fuse, leading to karyogamy. Each zygospore can contain several diploid nuclei. The developing diploid **zygospores** have thick coats that protect them from desiccation and other hazards. They may remain dormant until environmental conditions are favorable. When the zygospore germinates, it undergoes meiosis and produces haploid spores, which will, in turn, grow into a new organism. This form of sexual reproduction in fungi is called conjugation (although it differs markedly from conjugation in bacteria and protists), giving rise to the name “conjugated fungi”.





(a) (b)

Ascospores. The bright field light micrograph shows ascospores being released from asci in the fungus *Talaromyces flavus* var. *flavus*. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data

from Matt Russell)

Ascomycota: The Sac Fungi

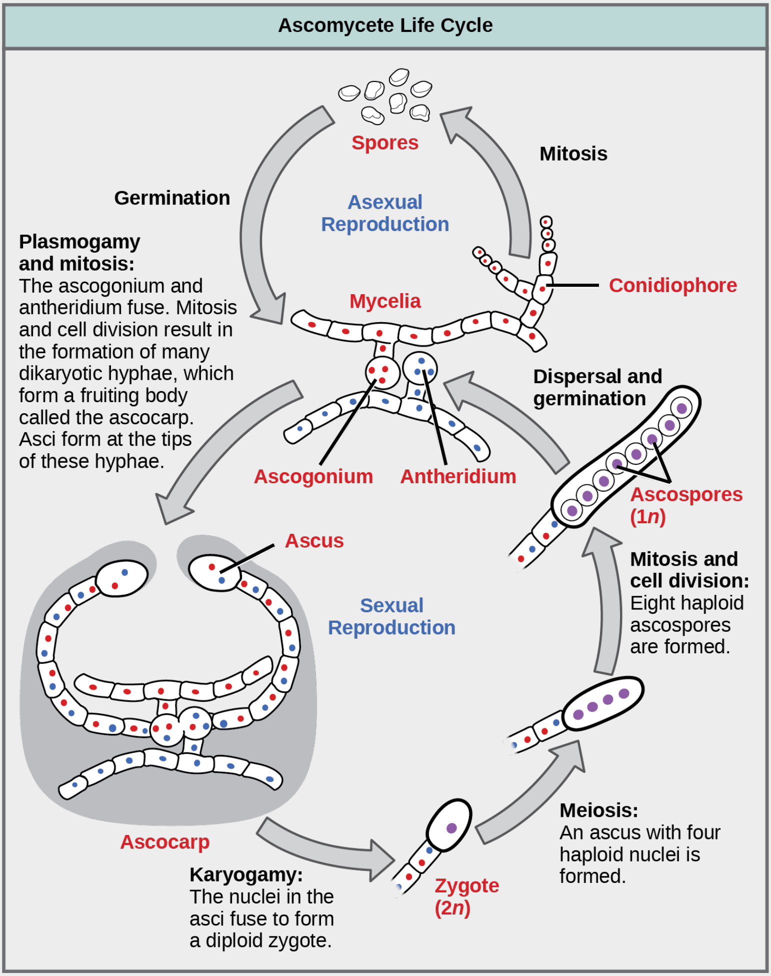
The majority of known fungi belong to the Phylum **Ascomycota**, which is characterized by the formation of an **ascus** (plural, asci), a sac-like structure that contains haploid *ascospores*. Filamentous ascomycetes produce hyphae divided by perforated septa, allowing streaming of cytoplasm from one cell to another. Conidia and asci, which are used respectively for asexual and sexual reproduction, are usually separated from the vegetative hyphae by blocked (non-perforated) septa. Many ascomycetes are of commercial importance. Some play a beneficial role for humanity, such as the yeasts used in baking, brewing, and wine fermentation, and directly as food delicacies such as truffles and morels. *Aspergillus oryzae* is used in the fermentation of rice to produce sake. Other ascomycetes parasitize plants and animals, including humans. For example, fungal pneumonia poses a significant threat to AIDS patients who have a compromised immune system. Ascomycetes not only infest and destroy crops directly; they also produce poisonous secondary metabolites that make crops unfit for consumption.

Asexual reproduction is frequent and involves the production of conidiophores that release haploid *conidiospores* ([link]). Sexual reproduction starts

with the development of special hyphae from either one of two types of mating strains ([link]). The “male” strain produces an antheridium and the “female” strain develops an ascogonium. At fertilization, the antheridium and the ascogonium combine in plasmogamy, without nuclear fusion. Special dikaryotic ascogenous (ascus-producing) hyphae arise from this **dikaryon**, in which each cell has pairs of nuclei: one from the “male” strain and one from the “female” strain. In each ascus, two haploid nuclei fuse in karyogamy. Thousands of asci fill a fruiting body called the **ascocarp**. The diploid nucleus in each ascus gives rise to haploid nuclei by meiosis, and spore walls form around each nucleus. The spores in each ascus contain the meiotic products of a single diploid nucleus. The ascospores are then released, germinate, and form hyphae that are disseminated in the environment and start new mycelia ([link]).

Visual Connection

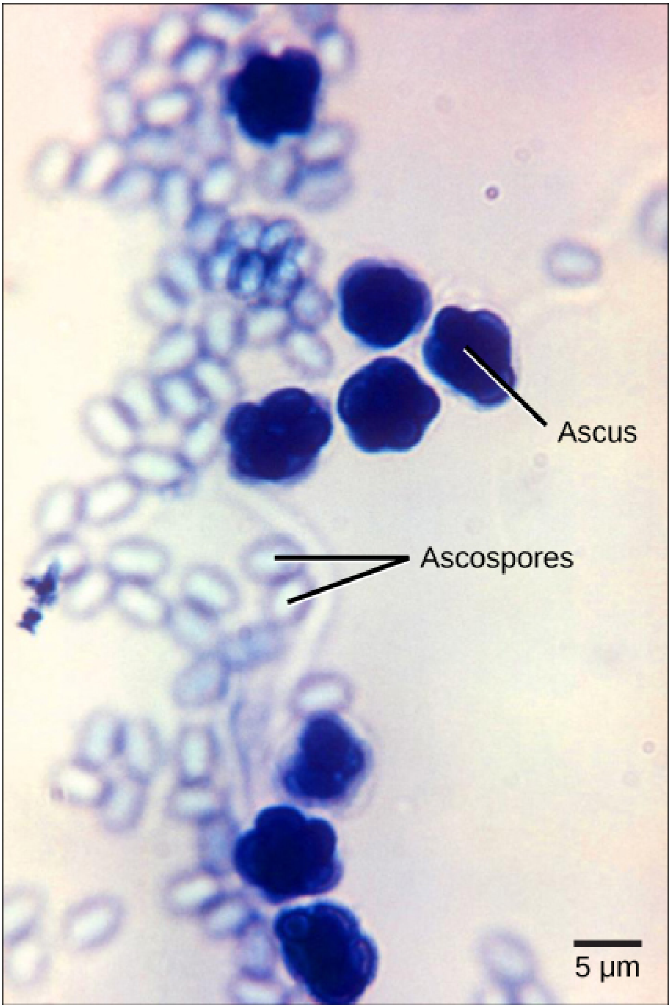
Ascomycete life cycle. The lifecycle of an ascomycete is characterized by the production of asci during the sexual phase. In each ascus, the four nuclei produced by meiosis divide once mitotically for a total of eight haploid ascospores. The haploid phase is the predominant phase of the life cycle in Ascomycetes.



Which of the following statements is true?

1. A dikaryotic ascus that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.
2. A diploid ascus that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.
3. A haploid zygote that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to

form eight ascospores.
4. A dikaryotic ascus that forms in the ascocarp undergoes plasmogamy, meiosis, and mitosis to form eight ascospores.



Fairy ring. The fruiting bodies of a basidiomycete form a ring in a meadow, commonly called "fairy

ring.” The best-known fairy ring fungus has the scientific name *Marasmius oreades*. The body of this fungus, its mycelium, is underground and grows outward in a circle. As it grows, the mycelium depletes the soil of nitrogen, causing the mycelia to grow away from the center and leading to the “fairy ring” of fruiting bodies where there is adequate soil nitrogen. (Credit: "Cropcircles"/Wikipedia Commons)]

Basidiomycota: The Club Fungi

The fungi in the Phylum **Basidiomycota** are easily recognizable under a light microscope by their club-shaped fruiting bodies called **basidia** (singular, **basidium**), which are the swollen terminal cells of hyphae. The basidia, which are the reproductive organs of these fungi, are often contained within the familiar mushroom, commonly seen in fields after rain, on the supermarket shelves, and growing on your lawn ([link]). These mushroom-producing basidiomycetes are sometimes referred to as *“gill fungi”* because of the presence of gill-like structures on the underside of the cap. The gills are actually *compacted hyphae* on which the basidia are borne. This group also includes shelf fungi, which cling to the bark of trees like small shelves. In addition, the basidiomycota include smuts and rusts, which are important plant pathogens. Most edible fungi belong to the Phylum Basidiomycota; however, some basidiomycota are inedible and produce deadly

toxins. For example, *Cryptococcus neoformans* causes severe respiratory illness. The infamous death cap mushroom (*Amanita phalloides*) is related to the fly agaric seen at the beginning of the previous section.

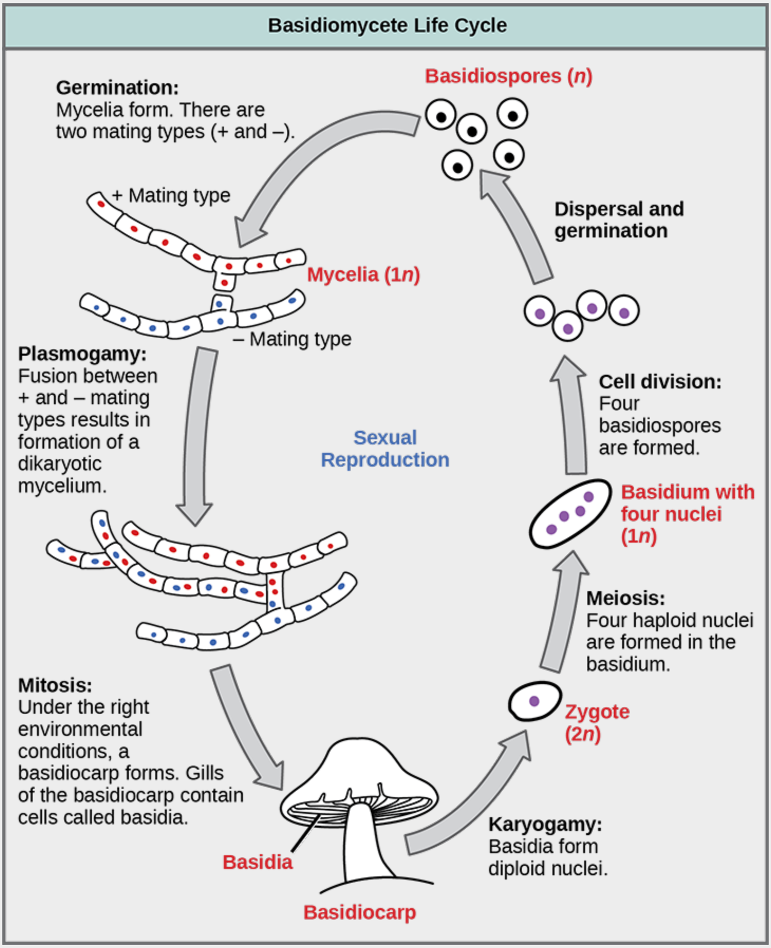
The lifecycle of basidiomycetes includes *alternation of generations* ([link]). Most fungi are haploid through most of their life cycles, but the basidiomycetes produce *both* haploid and dikaryotic mycelia, with the dikaryotic phase being dominant. (Note: The dikaryotic phase is technically not diploid, since the nuclei remain unfused until shortly before spore production.) In the basidiomycetes, sexual spores are more common than asexual spores. The sexual spores form in the club-shaped basidium and are called basidiospores. In the basidium, nuclei of two different mating strains fuse (karyogamy), giving rise to a diploid

zygote that then undergoes meiosis. The haploid nuclei migrate into four different chambers appended to the basidium, and then become basidiospores.

Each basidiospore germinates and generates *monokaryotic haploid hyphae*. The mycelium that results is called a primary mycelium. Mycelia of different mating strains can combine and produce a secondary mycelium that contains haploid nuclei of two different mating strains. This is the dominant dikaryotic stage of the basidiomycete life cycle. Thus, each cell in this mycelium has two haploid nuclei, which will not fuse until formation of the basidium. Eventually, the secondary mycelium generates a **basidiocarp**, a fruiting body that protrudes from the ground—this is what we think of as a mushroom. The basidiocarp bears the developing basidia on the gills under its cap.

Visual Connection

Basidiomycete life cycle. The lifecycle of a basidiomycete has alternate generations with haploid and dikaryotic mycelia. Haploid primary mycelia fuse to form a dikaryotic secondary mycelium, which is the dominant stage of the life cycle, and produces the basidiocarp.



Which of the following statements is true?

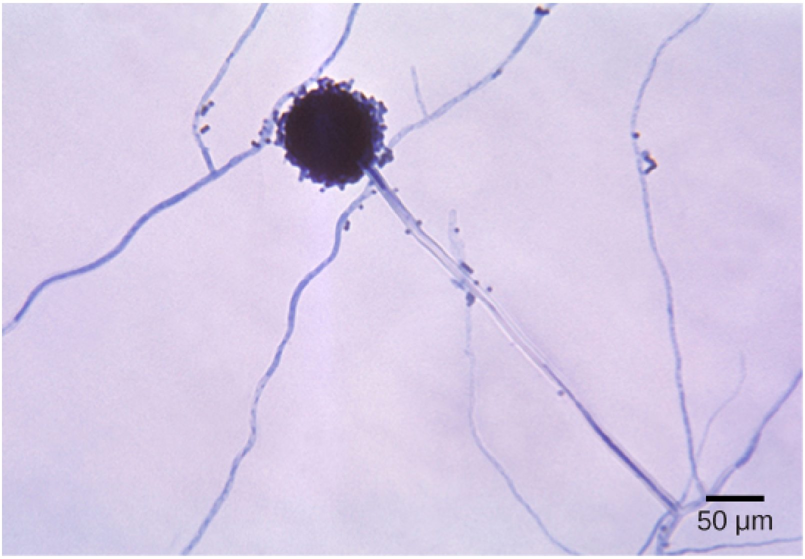
1. A basidium is the fruiting body of a mushroom-producing fungus, and it forms four basidiocarps.
2. The result of the plasmogamy step is four basidiospores.
3. Karyogamy results directly in the formation of mycelia.
4. A basidiocarp is the fruiting body of a

mushroom-producing fungus.

Aspergillus. *Aspergillus niger* is an asexually reproducing fungus (phylum Ascomycota) commonly found as a food contaminant. The spherical structure in this light micrograph is an asexual conidiophore. Molecular studies have placed *Aspergillus* with the ascomycetes and sexual cycles have been identified in some species. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

Asexual Ascomycota and Basidiomycota

Imperfect fungi—those that do not display a sexual phase—were formerly classified in the form phylum **Deuteromycota**, an invalid taxon no longer used in the present, ever-developing classification of organisms. While Deuteromycota was once a classification taxon, recent molecular analysis has shown that some of the members classified in this group belong to the Ascomycota ([link]) or the Basidiomycota. Because some members of this group have not yet been appropriately classified, they are less well described in comparison to members of other fungal taxa. Most imperfect fungi live on land, with a few aquatic exceptions. They form visible mycelia with a fuzzy appearance and are commonly known as **mold**.



The fungi in this group have a large impact on everyday human life. The food industry relies on them for ripening some cheeses. The blue veins in Roquefort cheese and the white crust on Camembert are the result of fungal growth. The antibiotic penicillin was originally discovered on an overgrown Petri plate, on which a colony of *Penicillium* fungi had killed the bacterial growth surrounding it. Other fungi in this group cause serious diseases, either directly as parasites (which infect both plants and humans), or as producers of potent toxic compounds, as seen in the aflatoxins released by fungi of the genus *Aspergillus*.

Glomeromycota

The **Glomeromycota** is a newly established phylum that comprises about 230 species, all of which are involved in close associations with the roots of trees. Fossil records indicate that trees and their root symbionts share a long evolutionary history. It appears that nearly all members of this family form **arbuscular mycorrhizae**: the hyphae interact with the root cells forming a mutually beneficial association in which the plants supply the carbon source and energy in the form of carbohydrates to the fungus, and the fungus supplies essential minerals from the soil to the plant. The exception is *Geosiphon pyriformis*, which hosts the cyanobacterium *Nostoc* as an endosymbiont.

The glomeromycetes do not reproduce sexually and do not survive without the presence of plant roots. Although they have coenocytic hyphae like the zygomycetes, they do not form zygospores. DNA analysis shows that all glomeromycetes probably descended from a common ancestor, making them a monophyletic lineage.

Section Summary

Chytridiomycota (chytrids) are considered the most ancestral group of fungi. They are mostly aquatic, and their gametes are the only fungal cells known to have flagella. They reproduce both sexually and asexually; the asexual spores are called zoospores.

Zygomycota (conjugated fungi) produce non-septate hyphae with many nuclei. Their hyphae fuse during sexual reproduction to produce a zygospore in a zygosporangium. Ascomycota (sac fungi) form spores in sacs called asci during sexual reproduction. Asexual reproduction is their most common form of reproduction. In the Basidiomycota (club fungi), the sexual phase predominates, producing showy fruiting bodies that contain club-shaped basidia, within which spores form. Most familiar mushrooms belong to this division. Fungi that have no known sexual cycle were originally classified in the “form phylum” Deuteromycota, but many have been classified by comparative molecular analysis with the Ascomycota and Basidiomycota. Glomeromycota form tight associations (called mycorrhizae) with the roots of plants.

Visual Connection Questions

[link] Which of the following statements is true?

1. A dikaryotic ascus that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.
2. A diploid ascus that forms in the ascocarp

undergoes karyogamy, meiosis, and mitosis to form eight ascospores.
3. A haploid zygote that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.
4. A dikaryotic ascus that forms in the ascocarp undergoes plasmogamy, meiosis, and mitosis to form eight ascospores.

[link] A

[link] Which of the following statements is true?

1. A basidium is the fruiting body of a mushroom-producing fungus, and it forms four basidiocarps.
2. The result of the plasmogamy step is four basidiospores.
3. Karyogamy results directly in the formation of mycelia.
4. A basidiocarp is the fruiting body of a mushroom-producing fungus.

[link] D

Review Questions

The most primitive phylum of fungi is the _____.

1. Chytridiomycota
2. Zygomycota
3. Glomeromycota
4. Ascomycota

A

Members of which phylum produce a club-shaped structure that contains spores?

1. Chytridiomycota
2. Basidiomycota
3. Glomeromycota
4. Ascomycota

B

Members of which phylum establish a successful symbiotic relationship with the roots of trees?

1. Ascomycota
2. Deuteromycota
3. Basidiomycota

4. Glomeromycota

D

The fungi that do not reproduce sexually used to be classified as ______.

1. Ascomycota
2. Deuteromycota
3. Basidiomycota
4. Glomeromycota

B

A scientist discovers a new species of fungus that introduces genetic diversity during reproduction by creating a diploid zygote. This new species cannot belong to which modern phylum of fungi?

1. Zygomycota
2. Glomeromycota
3. Chytridiomycota
4. Deuteromycota

B

Critical Thinking Questions

What is the advantage for a basidiomycete to produce a showy and fleshy fruiting body?

By ingesting spores and disseminating them in the environment as waste, animals act as agents of dispersal. The benefit to the fungus outweighs the cost of producing fleshy fruiting bodies.

For each of the four groups of perfect fungi (Chytridiomycota, Zygomycota, Ascomycota, and Basidiomycota), compare the body structure and features, and provide an example.

Chytridiomycota (Chytrids) may have a unicellular or multicellular body structure; some are aquatic with motile spores with flagella; an example is the *Allomyces*. Zygomycota (conjugated fungi) have a multicellular body structure; features include zygospores and presence in soil; examples are bread and fruit molds. Ascomycota (sac fungi) may have unicellular or multicellular body structure; a feature is sexual spores in sacs (asci); examples include the yeasts used in

bread, wine, and beer production.
Basidiomycota (club fungi) have multicellular bodies; features includes sexual spores in the basidiocarp (mushroom) and that they are mostly decomposers; mushroom-producing fungi are an example.

Glossary

Arbuscular mycorrhizae
: mycorrhizae commonly involving Glomeromycetes in which the fungal hyphae penetrate the cell walls of the plant root cells (but not the cell membranes)

ascocarp
: fruiting body of ascomycetes

Ascomycota
: (also, sac fungi) phylum of fungi that store spores in a sac called ascus

basidiocarp
: fruiting body that protrudes from the ground and bears the basidia

Basidiomycota
: (also, club fungi) phylum of fungi that produce club-shaped structures (basidia) that contain spores

basidium
: club-shaped fruiting body of basidiomycetes

Chytridiomycota
: (also, chytrids) primitive phylum of fungi that live in water and produce gametes with flagella

Deuteromycota
: former form phylum of fungi that do not have a known sexual reproductive cycle (presently members of two phyla: Ascomycota and Basidiomycota)

Ectomycorrhizae
: mycorrhizae in which the fungal hyphae do not penetrate the root cells of the plant

Glomeromycota
: phylum of fungi that form symbiotic relationships with the roots of trees

mold
: tangle of visible mycelia with a fuzzy appearance

Zygomycota
: (also, conjugated fungi) phylum of fungi that form a zygote contained in a zygospore

zygospore
: structure with thick cell wall that contains the

zygote in zygomycetes

Ecology of Fungi
By the end of this section, you will be able to do the following:

- Describe the role of fungi in various ecosystems
- Describe mutualistic relationships of fungi with plant roots and photosynthetic organisms
- Describe the beneficial relationship between some fungi and insects

Fungi play a crucial role in the constantly changing “balance” of ecosystems. They colonize most habitats on Earth, preferring dark, moist conditions. They can thrive in seemingly hostile environments, such as the tundra, thanks to a most successful symbiosis with photosynthetic organisms like algae to produce lichens. Within their communities, fungi are not as obvious as are large animals or tall treas. Like bacteria, they act behind the scene as major decomposers. With their versatile metabolism, fungi break down organic matter, which would otherwise not be recycled.

Habitats

Although fungi are primarily associated with humid and cool environments that provide a supply of organic matter, they colonize a surprising diversity of habitats, from seawater to human skin and

mucous membranes. Chytrids are found primarily in aquatic environments. Other fungi, such as *Coccidioides immitis*, which causes pneumonia when its spores are inhaled, thrive in the dry and sandy soil of the southwestern United States. Fungi that parasitize coral reefs live in the ocean. However, most members of the Kingdom Fungi grow on the forest floor, where the dark and damp environment is rich in decaying debris from plants and animals. In these environments, fungi play a major role as decomposers and recyclers, making it possible for members of the other kingdoms to be supplied with nutrients and live.

Bracket fungi. Fungi are an important part of ecosystem nutrient cycles. These bracket fungi growing on the side of a tree are the fruiting structures of a basidiomycete. They receive their nutrients through their hyphae, which invade and decay the tree trunk. (credit: Cory Zanker) Shelf fungi. Shelf fungi, so called because they grow on trees in a stack, attack and digest the trunk or branches of a tree. While some shelf fungi are found only on dead trees, others can parasitize living trees and cause eventual death, so they are considered serious tree pathogens. (credit: Cory Zanker)

Decomposers and Recyclers

The food web would be incomplete without organisms that decompose organic matter ([link]). Some elements—such as nitrogen and phosphorus—

are required in large quantities by biological systems, and yet are not abundant in the environment. The action of fungi releases these elements from decaying matter, making them available to other living organisms. Trace elements present in low amounts in many habitats are essential for growth, and would remain tied up in rotting organic matter if fungi and bacteria did not return them to the environment via their metabolic activity.

The ability of fungi to degrade many large and insoluble molecules is due to their mode of nutrition. As seen earlier, digestion precedes ingestion. Fungi produce a variety of exoenzymes to digest nutrients. The enzymes are either released into the substrate or remain bound to the outside of the fungal cell wall. Large molecules are broken down into small molecules, which are transported

into the cell by a system of protein carriers embedded in the cell membrane. Because the movement of small molecules and enzymes is dependent on the presence of water, active growth depends on a relatively high percentage of moisture in the environment.

As saprobes, fungi help maintain a sustainable ecosystem for the animals and plants that share the same habitat. In addition to replenishing the environment with nutrients, fungi interact directly with other organisms in beneficial, and sometimes damaging, ways ([link]).

Mycorrhizae. The (a) infection of *Pinus radiata* (Monterey pine) roots by the hyphae of *Amanita muscaria* (fly amanita) causes the pine tree to produce many small, branched rootlets. The *Amanita* hyphae cover these small roots with a white mantle. (b) Spores (the round bodies) and hyphae (thread-like structures) are evident in this light micrograph

of an arbuscular mycorrhiza by a fungus on the root of a corn plant. (credit a: modification of work by Randy Molina, USDA; credit b: modification of work by Sara Wright, USDA-ARS; scale-bar data from Matt Russell) Lichens. Lichens have many forms. They may be (a) crust-like, (b) hair-like, or (c) leaf-like. (credit a: modification of work by Jo Naylor; credit b: modification of work by "djpmapleferryman"/Flickr; credit c: modification of work by Cory Zanker) Structure of a lichen. This cross-section of a lichen thallus shows the (a) upper cortex of fungal hyphae, which provides protection; the (b) algal zone where photosynthesis occurs, the (c) medulla of fungal hyphae, and the (d) lower cortex, which also provides protection and may have (e) *rhizines* to anchor the thallus to the substrate. Leaf-cutter ant. A leaf-cutter ant transports a leaf that will feed a farmed fungus. (credit: Scott Bauer, USDA-ARS)

Mutualistic Relationships

Symbiosis is the ecological interaction between two organisms that live together. This definition does not describe the type or quality of the interaction. When both members of the association benefit, the symbiotic relationship is called mutualistic. Fungi form mutualistic associations with many types of organisms, including cyanobacteria, algae, plants, and animals.

Fungus/Plant Mutualism

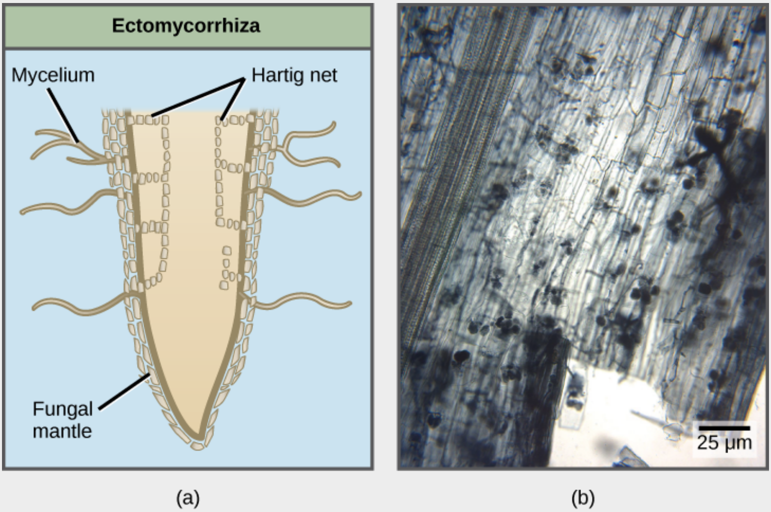
One of the most remarkable associations between fungi and plants is the establishment of *mycorrhizae*. **Mycorrhiza**, which is derived from the Greek words *myco* meaning fungus and *rhizo* meaning root, refers to the fungal partner of a mutualistic association between vascular plant roots and their symbiotic fungi. Nearly 90 percent of all vascular plant species have mycorrhizal partners. In a mycorrhizal association, the fungal mycelia use their extensive network of hyphae and large surface area in contact with the soil to channel water and minerals from the soil into the plant. In exchange, the plant supplies the products of photosynthesis to fuel the metabolism of the fungus.

There are several basic types of mycorrhizae. **Ectomycorrhizae** (“outside” mycorrhizae) depend on fungi enveloping the roots in a sheath (called a mantle). Hyphae grow from the mantle into the root and envelope the outer layers of the root cells in a network of hyphae called a *Hartig net* ([link]). The fungal partner can belong to the Ascomycota, Basidiomycota or Zygomycota. **Endomycorrhizae** ("inside" mycorrhizae), also called *arbuscular mycorrhizae*, are produced when the fungi grow inside the root in a branched structure called an *arbuscule* (from the Latin for “little trees”). The fungal partners of endomycorrhizal associates all belong to the Glomeromycota. The fungal

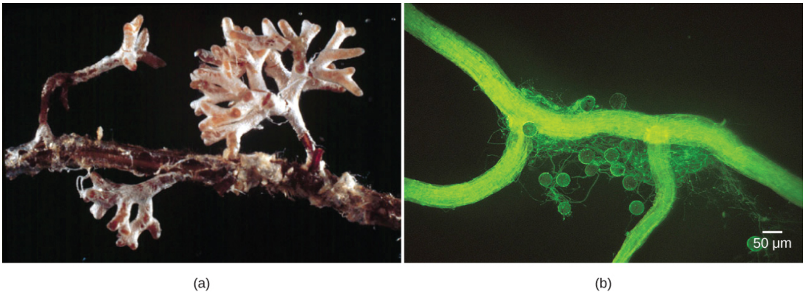
arbuscules penetrate root cells between the cell wall and the plasma membrane and are the site of the metabolic exchanges between the fungus and the host plant ([link]**b** and [link]**b**). Orchids rely on a third type of mycorrhiza. Orchids are epiphytes that typically produce very small airborne seeds without much storage to sustain germination and growth. Their seeds will not germinate without a mycorrhizal partner (usually a Basidiomycete). After nutrients in the seed are depleted, fungal symbionts support the growth of the orchid by providing necessary carbohydrates and minerals. Some orchids continue to be mycorrhizal throughout their life cycle.

Visual Connection

Two types of mycorrhizae. (a) Ectomycorrhizae and (b) arbuscular or endomycorrhizae have different mechanisms for interacting with the roots of plants. (credit b: MS Turmel, University of Manitoba, Plant Science Department)



If symbiotic fungi were absent from the soil, what impact do you think this would have on plant growth?



Other examples of fungus–plant mutualism include the endophytes: fungi that live inside tissue without damaging the host plant. Endophytes release toxins that repel herbivores, or confer resistance to environmental stress factors, such as infection by microorganisms, drought, or heavy metals in soil.

Evolution Connection

Coevolution of Land Plants and Mycorrhizae

As we have seen, mycorrhizae are the fungal partners of a mutually beneficial symbiotic association that coevolved between roots of vascular plants and fungi. A well-supported theory proposes that fungi were instrumental in the evolution of the root system in plants and contributed to the success of Angiosperms. The bryophytes (mosses and liverworts), which are considered the most ancestral plants and the first to survive and adapt on land, have simple underground rhizoids, rather than a true root system, and therefore cannot survive in dry areas. However, some bryophytes have arbuscular mycorrhizae and some do not.

True roots first appeared in the ancestral vascular plants: Vascular plants that developed a system of thin extensions from their roots would have had a selective advantage over nonvascular plants because they had a greater surface area of contact with the fungal partners than did the rhizoids of mosses and liverworts. The first true roots would have allowed vascular plants to obtain more water and nutrients in the ground.

Fossil records indicate that fungi actually preceded the invasion of ancestral freshwater plants onto dry land. The first association between fungi and photosynthetic organisms on land involved moss-like plants and endophytes. These early associations developed before roots appeared in

plants. Slowly, the benefits of the endophyte and rhizoid interactions for both partners led to present-day mycorrhizae: About 90 percent of today's vascular plants have associations with fungi in their rhizosphere.

The fungi involved in mycorrhizae display many characteristics of ancestral fungi; they produce simple spores, show little diversification, do not have a sexual reproductive cycle, and cannot live outside of a mycorrhizal association. The plants benefited from the association because mycorrhizae allowed them to move into new habitats and allowed the increased uptake of nutrients, which gave them an enormous selective advantage over plants that did not establish symbiotic relationships.

Lichens

Lichens display a range of colors and textures ([link]) and can survive in the most unusual and hostile habitats. They cover rocks, gravestones, tree bark, and the ground in the tundra where plant roots cannot penetrate. Lichens can survive extended periods of drought, when they become completely desiccated, and then rapidly become active once water is available again.

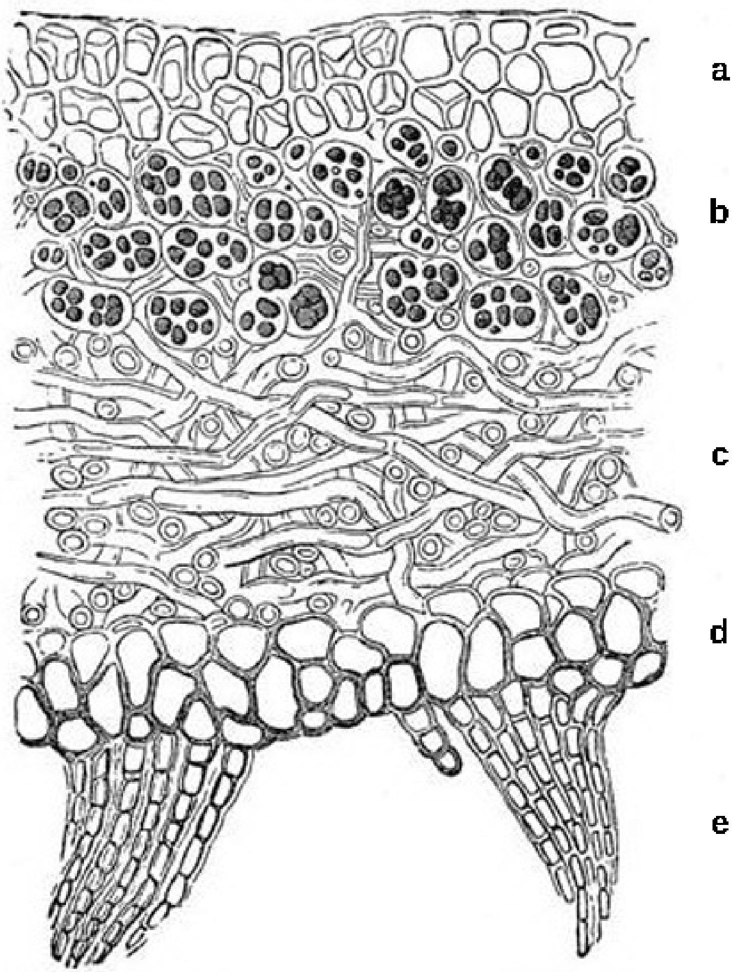
Link to Learning

Explore the world of lichens using this site from Oregon State University.

(a) (b) (c)

It is important to note that lichens are *not* a single organism, but rather another wonderful example of a mutualism, in which a fungus (usually a member of the Ascomycota or Basidiomycota) lives in a physical and physiological relationship with a photosynthetic organism (a eukaryotic alga or a prokaryotic cyanobacterium) ([link]). Generally, neither the fungus nor the photosynthetic organism can survive alone outside of the symbiotic relationship. The body of a lichen, referred to as a thallus, is formed of hyphae wrapped around the photosynthetic partner. The photosynthetic organism provides carbon and energy in the form of carbohydrates. Some cyanobacteria additionally fix nitrogen from the atmosphere, contributing nitrogenous compounds to the association. In return, the fungus supplies minerals and protection from dryness and excessive light by encasing the algae in its mycelium. The fungus also attaches the

lichen to its substrate.



The thallus of lichens grows very slowly, expanding its diameter a few millimeters per year. Both the fungus and the alga participate in the formation of dispersal units, called soredia—clusters of algal cells surrounded by mycelia. Soredia are dispersed by wind and water and form new lichens.

Lichens are extremely sensitive to air pollution, especially to abnormal levels of nitrogenous and sulfurous compounds. The U.S. Forest Service and National Park Service can monitor air quality by measuring the relative abundance and health of the lichen population in an area. Lichens fulfill many ecological roles. Caribou and reindeer eat lichens, and they provide cover for small invertebrates that hide in the mycelium. In the production of textiles, weavers used lichens to dye wool for many centuries until the advent of synthetic dyes. The pigments used in litmus paper are also extracted from lichens.

Link to Learning

Lichens are used to monitor the quality of air. Read more on this site from the United States Forest Service.

Fungus/Animal Mutualism

Fungi have evolved mutualisms with numerous insects in Phylum Arthropoda: joint-legged invertebrates with a chitinous exoskeleton. Arthropods depend on the fungus for protection from predators and pathogens, while the fungus obtains nutrients and a way to disseminate spores into new environments. The association between

species of Basidiomycota and scale insects is one example. The fungal mycelium covers and protects the insect colonies. The scale insects foster a flow of nutrients from the parasitized plant to the fungus.

In a second example, leaf-cutter ants of Central and South America literally farm fungi. They cut disks of leaves from plants and pile them up in subterranean gardens ([link]). Fungi are cultivated in these disk gardens, digesting the cellulose in the leaves that the ants cannot break down. Once smaller sugar molecules are produced and consumed by the fungi, the fungi in turn become a meal for the ants. The insects also patrol their garden, preying on competing fungi. Both ants and fungi benefit from this mutualistic association. The fungus receives a steady supply of leaves and freedom from competition, while the ants feed on the fungi they cultivate.

Fungivores

Animal dispersal is important for some fungi because an animal may carry fungal spores considerable distances from the source. Fungal spores are rarely completely degraded in the gastrointestinal tract of an animal, and many are able to germinate when they are passed in the feces. Some “dung fungi” actually require passage through the digestive system of herbivores to complete their lifecycle. The black truffle—a prized gourmet delicacy—is the fruiting body of an underground ascomycete. Almost all truffles are ectomycorrhizal, and are usually found in close association with

trees. Animals eat truffles and disperse the spores. In Italy and France, truffle hunters use female pigs to sniff out truffles (female pigs are attracted to truffles because the fungus releases a volatile compound closely related to a pheromone produced by male pigs.)

Section Summary

Fungi have colonized nearly all environments on Earth, but are frequently found in cool, dark, moist places with a supply of decaying material. Fungi are saprobes that decompose organic matter. Many successful mutualistic relationships involve a fungus and another organism. Many fungi establish complex mycorrhizal associations with the roots of plants. Some ants farm fungi as a supply of food. Lichens are a symbiotic relationship between a fungus and a photosynthetic organism, usually an alga or cyanobacterium. The photosynthetic organism provides energy from stored carbohydrates, while the fungus supplies minerals and protection. Some animals that consume fungi help disseminate spores over long distances.

Visual Connection Questions

[link] If symbiotic fungi are absent from the soil, what impact do you think this would have on plant growth?

[link] Without mycorrhiza, plants cannot absorb adequate nutrients, which stunts their growth. Addition of fungal spores to sterile soil can alleviate this problem.

Review Questions

What term describes the close association of a fungus with the root of a tree?

1. a rhizoid
2. a lichen
3. a mycorrhiza
4. an endophyte

C

Why are fungi important decomposers?

1. They produce many spores.
2. They can grow in many different

environments.
3. They produce mycelia.
4. They recycle carbon and inorganic minerals by the process of decomposition.

D

Consider an ecosystem where all the fungi not involved in mycorrhizae are eliminated. How would this affect nitrogen intake by plants?

1. Nitrogen intake would increase.
2. Nitrogen intake would not change.
3. Nitrogen intake would decrease.
4. Nitrogen intake would stop.

C

Critical Thinking Questions

Why does protection from light actually benefit the photosynthetic partner in lichens?

Protection from excess light that may bleach photosynthetic pigments allows the

photosynthetic partner to survive in environments unfavorable to plants.

Ambrosia bark beetles carry *Ambrosiella* fungal spores to trees, then bore holes and lay their eggs with the fungus. When the new larvae hatch, they eat the fungus that has germinated in the holes. Describe how this relationship can be classified as mutualistic.

The bark beetles and the fungus have a mutualistic relationship since each partner benefits from interacting with the other. The beetle can provide food for its offspring, while the fungus can spread to new trees.

Ecologists often attempt to introduce new plants to restore degraded land. In an arid climate, scientists recommend introducing plants with arbuscular mycorrhizae. How would the mycorrhizae increase the plants’ survival compared to plants without mycorrhizae?

Plants with arbuscular mycorrhizae are colonized by fungi that penetrate root cells, and exchange metabolites with the plant. The network of fungal hyphae extends from the root cells out into the environment, covering a

larger area than the plant's root system alone. This allows the plant to draw water from a larger area, increasing the likelihood that it can meet its daily needs.

Glossary

arbuscular mycorrhiza
: mycorrhizal association in which the fungal hyphae enter the root cells and form extensive networks

ectomycorrhiza
: mycorrhizal fungi that surround the roots with a mantle and have a Hartig net that extends into the roots between cells

lichen
: close association of a fungus with a photosynthetic alga or bacterium that benefits both partners

mycorrhiza
: mutualistic association between fungi and vascular plant roots

soredia
: clusters of algal cells and mycelia that allow lichens to propagate

Fungal Parasites and Pathogens

By the end of this section, you will be able to do the following:

- Describe some fungal parasites and pathogens of plants
- Describe the different types of fungal infections in humans
- Explain why antifungal therapy is hampered by the similarity between fungal and animal cells

Parasitism describes a symbiotic relationship in which one member of the association benefits at the expense of the other. Both parasites and pathogens harm the host; however, pathogens cause disease, damage to host tissues or physiology, whereas parasites usually do not, but can cause serious damage and death by competition for nutrients or other resources. **Commensalism** occurs when one member benefits without affecting the other.

Fungal pathogens. Some fungal pathogens include (a) green mold on grapefruit, (b) powdery mildew on a zinnia, (c) stem rust on a sheaf of barley, and (d) grey rot on grapes. In wet conditions *Botrytis cinerea,* the fungus that causes grey rot, can destroy a grape crop. However, controlled infection of grapes by *Botrytis* results in noble rot, a condition that produces strong and much-prized dessert wines. (credit a: modification of work by Scott Bauer, USDA-ARS; credit b: modification of work by Stephen Ausmus, USDA-ARS; credit c: modification

of work by David Marshall, USDA-ARS; credit d: modification of work by Joseph Smilanick, USDA-ARS)

Plant Parasites and Pathogens

The production of sufficient high-quality crops is essential to human existence. Unfortunately, plant diseases have ruined many crops throughout human agricultural history, sometimes creating widespread famine. Many plant pathogens are fungi that cause tissue decay and the eventual death of the host ([link]). In addition to destroying plant tissue directly, some plant pathogens spoil crops by producing potent toxins that can further damage and kill the host plant. Fungi are also responsible for food spoilage and the rotting of stored crops. For example, the fungus *Claviceps purpurea* causes ergot, a disease of cereal crops (especially of rye). Although the fungus reduces the yield of cereals, the effects of the ergot's alkaloid toxins on humans and animals are of much greater significance. In animals, the disease is referred to as *ergotism*. The most common signs and symptoms are convulsions, hallucination, gangrene, and loss of milk in cattle. The active ingredient of ergot is *lysergic acid*, which is a precursor of the drug LSD. Smuts, rusts, and powdery or downy mildew are other examples of common fungal pathogens that affect crops.

Aflatoxins are toxic, carcinogenic compounds released by fungi of the genus *Aspergillus*. Periodically, harvests of nuts and grains are tainted by aflatoxins, leading to massive recall of produce. This sometimes ruins producers and causes food shortages in developing countries.

Fungal diseases of humans. (a) Ringworm presents as a red ring on skin; (b) *Trichophyton violaceum*, shown in this bright field light micrograph, causes superficial mycoses on the scalp; (c) *Histoplasma capsulatum* is an ascomycete that infects airways and causes symptoms similar to influenza. (credit a:

modification of work by Dr. Lucille K. Georg, CDC; credit b: modification of work by Dr. Lucille K. Georg, CDC; credit c: modification of work by M. Renz, CDC; scale-bar data from Matt Russell)

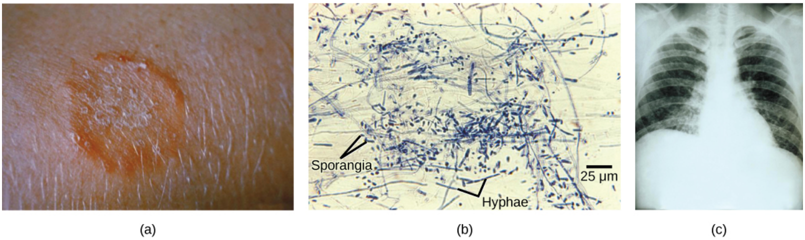
Animal and Human Parasites and Pathogens

Fungi can affect animals, including humans, in several ways. A **mycosis** is a fungal disease that results from infection and direct damage due to the growth and infiltration of the fungus. Fungi attack animals directly by colonizing and destroying tissues. **Mycotoxicosis** is the poisoning of humans (and other animals) by foods contaminated by fungal toxins (mycotoxins). **Mycetismus** specifically describes the ingestion of preformed toxins in poisonous mushrooms. In addition, individuals who display hypersensitivity to molds and spores may develop strong and dangerous allergic reactions. Fungal infections are generally very difficult to treat because, unlike bacteria, fungi are eukaryotes. Antibiotics only target prokaryotic cells, whereas compounds that kill fungi also harm the eukaryotic animal host.

Many fungal infections are *superficial*; that is, they occur on the animal’s skin. Termed *cutaneous* (“skin”) *mycoses*, they can have devastating effects. For example, the decline of the world’s frog population in recent years is caused (in part) by the

chytrid fungus *Batrachochytrium dendrobatidis*. This deadly fungus infects the skin of frogs and presumably interferes with cutaneous gaseous exchange, which is essential for amphibian survival. Similarly, more than a million bats in the United States have been killed by white-nose syndrome, which appears as a white ring around the mouth of the bat. It is caused by the cold-loving fungus *Pseudogymnoascus destructans*, which disseminates its deadly spores in caves where bats hibernate. Mycologists are researching the transmission, mechanism, and control of *P. destructans* to stop its spread.

Fungi that cause the superficial mycoses of the epidermis, hair, and nails rarely spread to the underlying tissue ([link]). These fungi are often misnamed “dermatophytes”, from the Greek words *dermis* meaning skin and *phyte* meaning plant, although they are not plants. Dermatophytes are also called *“ringworms”* because of the red ring they cause on skin. They secrete extracellular enzymes that break down *keratin* (a protein found in hair, skin, and nails), causing conditions such as athlete’s foot and jock itch. These conditions are usually treated with over-the-counter topical creams and powders, and are easily cleared. More persistent superficial mycoses may require prescription oral medications.



Systemic mycoses spread to internal organs, most commonly entering the body through the respiratory system. For example, *coccidioidomycosis* (often called valley fever) is commonly found in the southwestern United States, but as far north as Washington, where the fungus resides in the dust. Once inhaled, the spores develop in the lungs and cause symptoms similar to those of tuberculosis. *Histoplasmosis* is caused by the dimorphic fungus *Histoplasma capsulatum.* In its human host, *Histoplasma* grows as a yeast, causing pulmonary infections, and in rarer cases, swelling of the membranes of the brain and spinal cord. Treatment of these and many other fungal diseases requires the use of antifungal medications that have serious side effects.

Opportunistic mycoses are fungal infections that are either common in all environments, or part of the normal biota. They mainly affect individuals who have a compromised immune system. Patients in the late stages of AIDS suffer from opportunistic mycoses that can be life threatening. The yeast *Candida* sp., a common member of the natural biota, can grow unchecked and infect the vagina or mouth

(oral thrush) if the pH of the surrounding environment, the person's immune defenses, or the normal population of bacteria are altered.

Mycetismus can occur when poisonous mushrooms are eaten. It causes a number of human fatalities during mushroom-picking season. Many edible fruiting bodies of fungi resemble highly poisonous relatives, and amateur mushroom hunters are cautioned to carefully inspect their harvest and avoid eating mushrooms of doubtful origin. The adage "there are bold mushroom pickers and old mushroom pickers, but are there no old, bold mushroom pickers" is unfortunately true.

Scientific Method Connection

Dutch Elm Disease

Question: Do trees resistant to Dutch elm disease secrete antifungal compounds?

Hypothesis: Construct a hypothesis that addresses this question.

Background: Dutch elm disease is a fungal infestation that affects many species of elm (*Ulmus*) in North America. The fungus infects the vascular system of the tree, which blocks water flow within the plant and mimics drought stress. Accidently introduced to the United States in the early 1930s, it decimated American elm shade trees across the continent. It is caused by the fungus *Ophiostoma*

ulmi. The elm bark beetle acts as a vector and transmits the disease from tree to tree. Many European and Asiatic elms are less susceptible to the disease than are American elms.

Test the hypothesis: A researcher testing this hypothesis might do the following. Inoculate several Petri plates containing a medium that supports the growth of fungi with fragments of *Ophiostoma* mycelium. Cut (with a metal punch) several disks from the vascular tissue of susceptible varieties of American elms and resistant European and Asiatic elms. Include control Petri plates inoculated with mycelia without plant tissue to verify that the medium and incubation conditions do not interfere with fungal growth. As a positive control, add paper disks impregnated with a known fungicide to Petri plates inoculated with the mycelium.

Incubate the plates for a set number of days to allow fungal growth and spreading of the mycelium over the surface of the plate. Record the diameter of the zone of clearing, if any, around the tissue samples and the fungicide control disk. Record your observations in the following table.

Results of Antifungal Testing of Vascular

Tissue from Different Species of Elm Disk	Zone of Inhibition (mm)
Distilled Water	
Fungicide	
Tissue from Susceptible Elm #1	
Tissue from Susceptible Elm #2	
Tissue from Resistant Elm #1	
Tissue from Resistant Elm #2	

Analyze the data and report the results. Compare the effect of distilled water to the fungicide. These are negative and positive controls that validate the experimental setup. The fungicide should be surrounded by a clear zone where the fungus growth was inhibited. Is there a difference among different species of elm?

Draw a conclusion: Was there antifungal activity as expected from the fungicide? Did the results support the hypothesis? If not, how can this be explained? There are several possible explanations.

Section Summary

Fungi establish parasitic relationships with plants and animals. Fungal diseases can decimate crops and spoil food during storage. Compounds produced by fungi can be toxic to humans and other animals. Mycoses are infections caused by fungi. Superficial mycoses affect the skin, whereas systemic mycoses spread through the body. Fungal infections are difficult to cure, since fungi, like their hosts, are eukaryotic, and cladistically related closely to Kingdom Animalia.

Review Questions

A fungus that climbs up a tree reaching higher elevation to release its spores in the wind and does not receive any nutrients from the tree or contribute to the tree's welfare is described as a _____.

1. commensal
2. mutualist
3. parasite
4. pathogen

A

A fungal infection that affects nails and skin is classified as ______.

1. systemic mycosis
2. mycetismus
3. superficial mycosis
4. mycotoxicosis

C

The targets for anti-fungal drugs are much more limited than antibiotics or anti-viral medications. Why?

1. There are more bacteria and viruses than fungi.
2. Fungi can only be targeted during sexual reproduction, while bacteria and viruses can be targeted at any point in their lifespan.
3. Fungi cause topical infections, while viruses and bacteria cause systemic infections.
4. Human cells are much more similar to fungi cells than bacteria or viruses.

D

Critical Thinking Questions

Why can superficial mycoses in humans lead to bacterial infections?

Dermatophytes that colonize skin break down the keratinized layer of dead cells that protects tissues from bacterial invasion. Once the integrity of the skin is breached, bacteria can enter the deeper layers of tissues and cause infections.

Explain how the Red Queen Hypothesis describes the continuously evolving relationship between red grapes and *Botrytis cinerea*.

The Red Queen Hypothesis describes the biological stalemate between a predator and prey. The two populations are constantly applying evolutionary pressure on each other, forcing each population to adapt to counter an adaptation of the other population. In the case of the fungi *B. cinerea* and the red grape plant, the grapes are the prey and the fungi are the predator in the Red Queen Hypothesis. The grapes develop defenses to prevent infection by the fungi, ensuring that the *B. cinerea* that

survive to colonize the red grapes have developed adaptations to overcome the plant defenses. The red grapes that then survive the infection are the plants that have additional adaptations that limit the pathogenicity of *B. cinerea*. This cycle continues to repeat unless one population evolves an adaptation that cannot be countered by the other population, which would wipe out the later population.

Glossary

commensalism
: symbiotic relationship in which one member benefits while the other member is not affected

mycetismus
: ingestion of toxins in poisonous mushrooms

mycosis
: fungal infection

mycotoxicosis
: poisoning by a fungal toxin released in food

parasitism
: symbiotic relationship in which one member of the association benefits at the expense of the other

Importance of Fungi in Human Life

By the end of this section, you will be able to:

- Describe the importance of fungi to the balance of the environment
- Summarize the role of fungi in food and beverage preparation
- Describe the importance of fungi in the chemical and pharmaceutical industries
- Discuss the role of fungi as model organisms

Although we often think of fungi as organisms that cause disease and rot food, fungi are important to human life on many levels. As we have seen, they influence the well-being of human populations on a large scale because they are part of the nutrient cycle in ecosystems. They have other ecosystem roles as well. As animal pathogens, fungi help to control the population of damaging pests. These fungi are very specific to the insects they attack, and do not infect animals or plants. Fungi are currently under investigation as potential microbial insecticides, with several already on the market. For example, the fungus *Beauveria bassiana* is a pesticide being tested as a possible biological control agent for the recent spread of emerald ash borer. It has been released in Michigan, Illinois, Indiana, Ohio, West Virginia and Maryland ([link]).

The emerald ash borer is an insect that attacks ash trees. It is in turn parasitized by a pathogenic fungus that holds promise as a biological insecticide. The

parasitic fungus appears as white fuzz on the body of the insect. (credit: Houping Liu, USDA Agricultural Research Service)

The mycorrhizal relationship between fungi and plant roots is essential for the productivity of farm land. Without the fungal partner in root systems, 80–90 percent of trees and grasses would not survive. Mycorrhizal fungal inoculants are available as soil amendments from gardening supply stores and are promoted by supporters of organic agriculture.

We also eat some types of fungi. Mushrooms figure prominently in the human diet. Morels, shiitake mushrooms, chanterelles, and truffles are considered delicacies ([link]). The humble meadow mushroom,

Agaricus campestris, appears in many dishes. Molds of the genus *Penicillium* ripen many cheeses. They originate in the natural environment such as the caves of Roquefort, France, where wheels of sheep milk cheese are stacked in order to capture the molds responsible for the blue veins and pungent taste of the cheese.

The morel mushroom is an ascomycete much appreciated for its delicate taste. (credit: Jason Hollinger)

Fermentation—of grains to produce beer, and of

fruits to produce wine—is an ancient art that humans in most cultures have practiced for millennia. Wild yeasts are acquired from the environment and used to ferment sugars into CO_2 and ethyl alcohol under anaerobic conditions. It is now possible to purchase isolated strains of wild yeasts from different wine-making regions. Louis Pasteur was instrumental in developing a reliable strain of brewer's yeast, *Saccharomyces cerevisiae*, for the French brewing industry in the late 1850s. This was one of the first examples of biotechnology patenting.

Many secondary metabolites of fungi are of great commercial importance. Antibiotics are naturally produced by fungi to kill or inhibit the growth of bacteria, limiting their competition in the natural environment. Important antibiotics, such as penicillin and the cephalosporins, are isolated from fungi. Valuable drugs isolated from fungi include the immunosuppressant drug cyclosporine (which reduces the risk of rejection after organ transplant), the precursors of steroid hormones, and ergot alkaloids used to stop bleeding. Psilocybin is a compound found in fungi such as *Psilocybe semilanceata* and *Gymnopilus junonius,* which have been used for their hallucinogenic properties by various cultures for thousands of years.

As simple eukaryotic organisms, fungi are important model research organisms. Many advances in

modern genetics were achieved by the use of the red bread mold *Neurospora crassa*. Additionally, many important genes originally discovered in *S. cerevisiae* served as a starting point in discovering analogous human genes. As a eukaryotic organism, the yeast cell produces and modifies proteins in a manner similar to human cells, as opposed to the bacterium *Escherichia coli,* which lacks the internal membrane structures and enzymes to tag proteins for export. This makes yeast a much better organism for use in recombinant DNA technology experiments. Like bacteria, yeasts grow easily in culture, have a short generation time, and are amenable to genetic modification.

Section Summary

Fungi are important to everyday human life. Fungi are important decomposers in most ecosystems. Mycorrhizal fungi are essential for the growth of most plants. Fungi, as food, play a role in human nutrition in the form of mushrooms, and also as agents of fermentation in the production of bread, cheeses, alcoholic beverages, and numerous other food preparations. Secondary metabolites of fungi are used as medicines, such as antibiotics and anticoagulants. Fungi are model organisms for the study of eukaryotic genetics and metabolism.

Review Questions

Yeast is a facultative anaerobe. This means that alcohol fermentation takes place only if:

1. the temperature is close to 37°C
2. the atmosphere does not contain oxygen
3. sugar is provided to the cells
4. light is provided to the cells

B

The advantage of yeast cells over bacterial cells to express human proteins is that:

1. yeast cells grow faster
2. yeast cells are easier to manipulate genetically
3. yeast cells are eukaryotic and modify proteins similarly to human cells
4. yeast cells are easily lysed to purify the proteins

C

Free Response

Historically, artisanal breads were produced by capturing wild yeasts from the air. Prior to the development of modern yeast strains, the production of artisanal breads was long and laborious because many batches of dough ended up being discarded. Can you explain this fact?

The dough is often contaminated by toxic spores that float in the air. It was one of Louis Pasteur’s achievements to purify reliable strains of baker’s yeast to produce bread consistently.

Features of the Animal Kingdom

By the end of this section, you will be able to do the following:

- List the features that distinguish the kingdom Animalia from other kingdoms
- Explain the processes of animal reproduction and embryonic development
- Describe the roles that Hox genes play in development

Two different groups within the Domain Eukaryota have produced complex multicellular organisms: The plants arose within the Archaeplastida, whereas the animals (and their close relatives, the fungi) arose within the Opisthokonta. However, plants and animals not only have different life styles, they also have different cellular histories as eukaryotes. The opisthokonts share the possession of a single posterior flagellum in flagellated cells, e.g., sperm cells.

Most animals also share other features that distinguish them from organisms in other kingdoms. All animals require a source of food and are therefore *heterotrophic*, ingesting other living or dead organisms. This feature distinguishes them from *autotrophic* organisms, such as most plants, which synthesize their own nutrients through photosynthesis. As heterotrophs, animals may be carnivores, herbivores, omnivores, or parasites

([link]**a,b**). As with plants, almost all animals have a complex tissue structure with differentiated and specialized tissues. The necessity to collect food has made most animals motile, at least during certain life stages. The typical life cycle in animals is diplontic (like you, the diploid state is multicellular, whereas the haploid state is gametic, such as sperm or egg). We should note that the alternation of generations characteristic of the land plants is typically not found in animals. In animals whose life histories include several to multiple body forms (e.g., insect larvae or the medusae of some Cnidarians), all body forms are diploid. Animal embryos pass through a series of developmental stages that establish a determined and fixed body plan. The **body plan** refers to the morphology of an animal, determined by developmental cues.
Heterotrophy. All animals are heterotrophs and thus derive energy from a variety of food sources. The (a) black bear is an omnivore, eating both plants and animals. The (b) heartworm *Dirofilaria immitis* is a parasite that derives energy from its hosts. It spends its larval stage in mosquitoes and its adult stage infesting the heart of dogs and other mammals, as shown here. (credit a: modification of work by USDA Forest Service; credit b: modification of work by Clyde Robinson)

(a)

(b)

Complex Tissue Structure

Many of the specialized tissues of animals are associated with the requirements and hazards of seeking and processing food. This explains why animals typically have evolved special structures associated with specific methods of food capture and complex digestive systems supported by accessory organs. Sensory structures help animals navigate their environment, detect food sources (and avoid becoming a food source for other animals!). Movement is driven by muscle tissue attached to supportive structures like bone or chitin, and is coordinated by neural communication. Animal cells may also have unique structures for intercellular communication (such as gap junctions). The evolution of nerve tissues and muscle tissues has resulted in animals' unique ability to rapidly sense and respond to changes in their environment. This allows animals to survive in environments

where they must compete with other species to meet their nutritional demands.

The tissues of animals differ from those of the other major multicellular eukaryotes, plants and fungi, because their cells don't have cell walls. However, cells of animal tissues may be embedded in an extracellular matrix (e.g., mature bone cells reside within a mineralized organic matrix secreted by the cells). In vertebrates, bone tissue is a type of connective tissue that supports the entire body structure. The complex bodies and activities of vertebrates demand such supportive tissues. Epithelial tissues cover and protect both external and internal body surfaces, and may also have secretory functions. Epithelial tissues include the epidermis of the integument, the lining of the digestive tract and trachea, as well as the layers of cells that make up the ducts of the liver and glands of advanced animals, for example. The different types of tissues in true animals are responsible for carrying out specific functions for the organism. This differentiation and specialization of tissues is part of what allows for such incredible animal diversity.

Just as there are multiple ways to be a eukaryote, there are multiple ways to be a multicellular animal. The animal kingdom is currently divided into five monophyletic clades: Parazoa or Porifera (sponges), Placozoa (tiny parasitic creatures that resemble

multicellular amoebae), Cnidaria (jellyfish and their relatives), Ctenophora (the comb jellies), and Bilateria (all other animals). The Placozoa ("flat animal") and Parazoa (“beside animal”) do not have specialized tissues derived from germ layers of the embryo; although they do possess specialized cells that act *functionally* like tissues. The Placozoa have only four cell types, while the sponges have nearly two dozen. The three other clades do include animals with specialized tissues derived from the germ layers of the embryo. In spite of their superficial similarity to Cnidarian medusae, recent molecular studies indicate that the Ctenophores are only distantly related to the Cnidarians, which together with the Bilateria constitute the Eumetazoa ("true animals"). When we think of animals, we usually think of Eumetazoa, since most animals fall into this category.

Link to Learning
Watch a presentation by biologist E.O. Wilson on the importance of diversity.

Development of a simple embryo. During embryonic development, the zygote undergoes a series of mitotic cell divisions, or cleavages, that subdivide the egg into smaller and smaller

blastomeres. Note that the 8-cell stage and the blastula are about the same size as the original zygote. In many invertebrates, the blastula consists of a single layer of cells around a hollow space. During a process called gastrulation, the cells from the blastula move inward on one side to form an inner cavity. This inner cavity becomes the primitive gut (archenteron) of the gastrula ("little gut") stage. The opening into this cavity is called the *blastopore*, and in some invertebrates it is destined to form the mouth. Insect metamorphosis. (a) The grasshopper undergoes incomplete metamorphosis. (b) The butterfly undergoes complete metamorphosis. (credit: S.E. Snodgrass, USDA)

Animal Reproduction and Development

Most animals are diploid organisms, meaning that their body (somatic) cells are diploid and haploid reproductive (gamete) cells are produced through meiosis. Some exceptions exist: for example, in bees, wasps, and ants, the male is haploid because it develops from unfertilized eggs. Most animals undergo sexual reproduction. However, a few groups, such as cnidarians, flatworms, and roundworms, may also undergo asexual reproduction, in which offspring originate from part of the parental body.

Processes of Animal Reproduction and

Embryonic Development

During sexual reproduction, the haploid gametes of the male and female individuals of a species combine in a process called fertilization. Typically, both male and female gametes are required: the small, motile male sperm fertilizes the typically much larger, sessile female egg. This process produces a diploid fertilized egg called a zygote.

Some animal species—including sea stars and sea anemones—are capable of asexual reproduction. The most common forms of asexual reproduction for stationary aquatic animals include *budding* and *fragmentation*, where part of a parent individual can separate and grow into a new individual. This type of asexual reproduction produces genetically identical offspring, which would appear to be disadvantageous from the perspective of evolutionary adaptability, simply because of the potential buildup of deleterious mutations.

In contrast, a form of uniparental reproduction found in some insects and a few vertebrates is called parthenogenesis (or "virgin beginning"). In this case, progeny develop from a gamete, but without fertilization. Because of the nutrients stored in eggs, only females produce parthenogenetic offspring. In some insects, unfertilized eggs develop into new male offspring. This type of sex determination is called haplodiploidy, since females are diploid (with

both maternal and paternal chromosomes) and males are haploid (with only maternal chromosomes). A few vertebrates, e.g., some fish, turkeys, rattlesnakes, and whiptail lizards, are also capable of parthenogenesis. In the case of turkeys and rattlesnakes, parthenogenetically reproducing females also produce only male offspring, but not because the males are haploid. In birds and rattlesnakes, the female is the heterogametic (ZW) sex, so the only surviving progeny of post-meiotic parthenogenesis would be ZZ males. In the whiptail lizards, on the other hand, only female progeny are produced by parthenogenesis. These animals may not be identical to their parent, although they have only maternal chromosomes. However, for animals that are limited in their access to mates, uniparental reproduction can ensure genetic propagation.

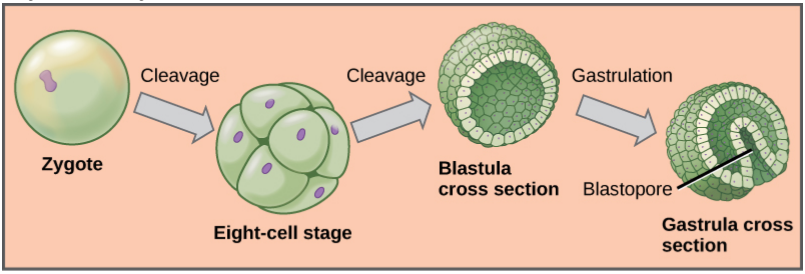
In animals, the zygote progresses through a series of developmental stages, during which primary **germ layers** (ectoderm, endoderm, and mesoderm) are established and reorganize to form an embryo. During this process, animal tissues begin to specialize and organize into organs and organ systems, determining their future morphology and physiology.

Animal development begins with **cleavage**, a series of mitotic cell divisions, of the zygote ([link]). Cleavage differs from somatic cell division in that the egg is subdivided by successive cleavages into

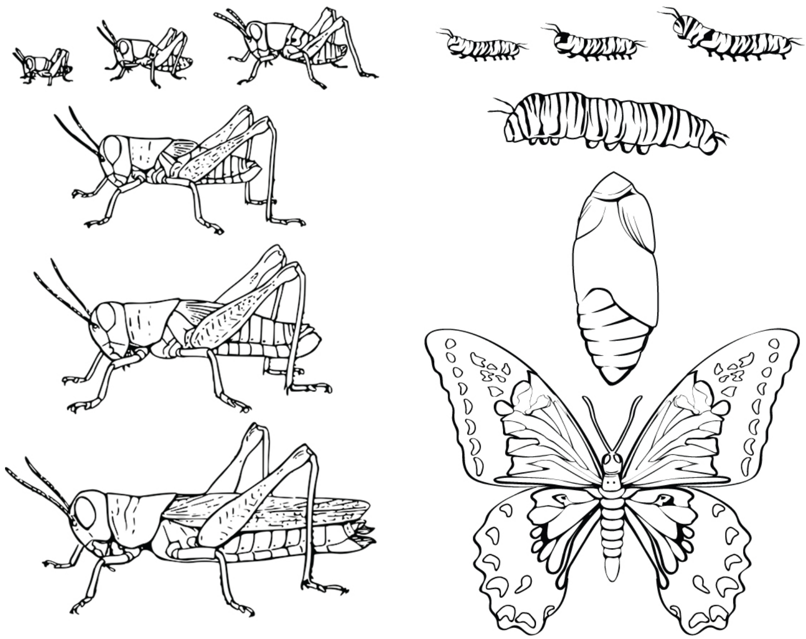
smaller and smaller cells, with *no* actual cell growth. The cells resulting from subdivision of the material of the egg in this way are called **blastomeres**. Three cell divisions transform the single-celled zygote into an eight-celled structure. After further cell division and rearrangement of existing cells, a solid morula is formed, followed by a hollow structure called a **blastula**. The blastula is hollow only in invertebrates whose eggs have relatively small amounts of yolk. In very yolky eggs of vertebrates, the yolk remains undivided, with most cells forming an embryonic layer on the surface of the yolk (imagine a chicken embryo growing over the egg's yolk), which serve as food for the developing embryo.

Further cell division and cellular rearrangement leads to a process called gastrulation. **Gastrulation** results in two important events: the formation of the primitive gut (archenteron) or digestive cavity, and the formation of the embryonic germ layers, as we have discussed above. These germ layers are programmed to develop into certain tissue types, organs, and organ systems during a process called **organogenesis**. *Diploblastic* organisms have two germ layers, endoderm and ectoderm. Endoderm forms the wall of the digestive tract, and ectoderm covers the surface of the animal. In *triploblastic* animals, a third layer forms: mesoderm, which differentiates into various structures between the ectoderm and endoderm, including the lining of the

body cavity.



Some animals produce larval forms that are different from the adult. In insects with *incomplete metamorphosis*, such as grasshoppers, the young resemble wingless adults, but gradually produce larger and larger wing buds during successive molts, until finally producing functional wings and sex organs during the last molt. Other animals, such as some insects and echinoderms, undergo complete metamorphosis in which the embryo develops into one or more feeding larval stages that may differ greatly in structure and function from the adult ([link]). The adult body then develops from one or more regions of larval tissue. For animals with complete metamorphosis, the larva and the adult may have different diets, limiting competition for food between them. Regardless of whether a species undergoes complete or incomplete metamorphosis, the series of developmental stages of the embryo remains largely the same for most members of the animal kingdom.



(a) Incomplete metamorphosis (b) Complete metamorphosis

Link to Learning

Watch the following video to see how human embryonic development (after the blastula and gastrula stages of development) reflects evolution.

The Role of Homeobox (*Hox*) Genes in Animal Development

Since the early nineteenth century, scientists have observed that many animals, from the very simple to the complex, shared similar embryonic

morphology and development. Surprisingly, a human embryo and a frog embryo, at a certain stage of embryonic development, look remarkably alike! For a long time, scientists did not understand why so many animal species looked similar during embryonic development but were very different as adults. They wondered what dictated the developmental direction that a fly, mouse, frog, or human embryo would take. Near the end of the twentieth century, a particular class of genes was discovered that had this very job. These genes that determine animal structure are called “homeotic genes,” and they contain DNA sequences called homeoboxes. Genes with homeoboxes encode protein transcription factors. One group of animal genes containing homeobox sequences is specifically referred to as ***Hox* genes**. This cluster of genes is responsible for determining the general body plan, such as the number of body segments of an animal, the number and placement of appendages, and animal head-tail directionality. The first *Hox* genes to be sequenced were those from the fruit fly (*Drosophila melanogaster*). A single *Hox* mutation in the fruit fly can result in an extra pair of wings or even legs growing from the head in place of antennae (this is because antennae and legs are embryologic homologous structures and their appearance as antennae or legs is dictated by their origination within specific body segments of the head and thorax during development). Now, *Hox* genes are known from virtually all other animals as

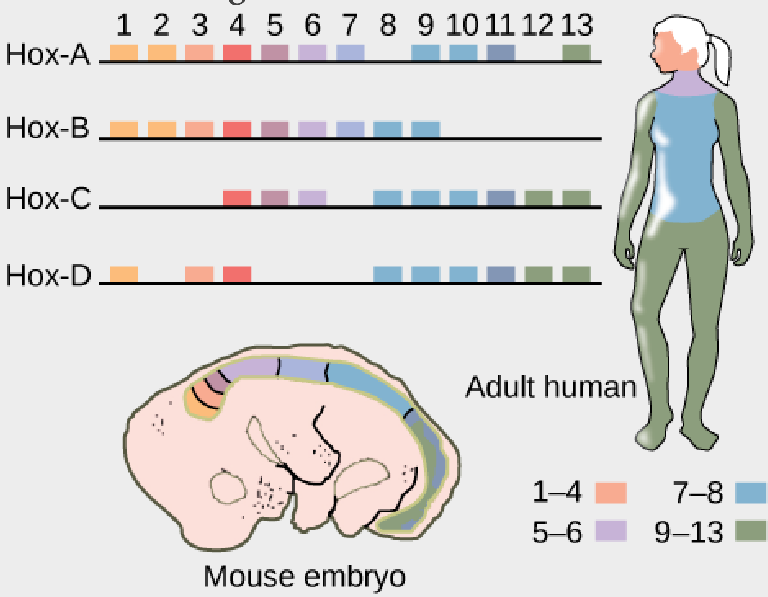
well.

While there are a great many genes that play roles in the morphological development of an animal, including other homeobox-containing genes, what makes *Hox* genes so powerful is that they serve as "master control genes" that can turn on or off large numbers of other genes. *Hox* genes do this by encoding transcription factors that control the expression of numerous other genes. *Hox* genes are homologous across the animal kingdom, that is, the genetic sequences of *Hox* genes and their positions on chromosomes are remarkably similar across most animals because of their presence in a common ancestor, from worms to flies, mice, and humans ([link]). In addition, the order of the genes reflects the anterior-posterior axis of the animal's body. One of the contributions to increased animal body complexity is that *Hox* genes have undergone at least two and perhaps as many as four duplication events during animal evolution, with the additional genes allowing for more complex body types to evolve. All vertebrates have four (or more) sets of *Hox* genes, while invertebrates have only one set.

Visual Connection

Hox genes. *Hox* genes are *highly conserved genes* encoding transcription factors that determine the course of embryonic development in animals. In

vertebrates, the genes have been duplicated into four clusters on *different chromosomes*: *Hox-A*, *Hox-B*, *Hox-C*, and *Hox-D*. Genes within these clusters are expressed in certain body segments at certain stages of development. Shown here is the homology between *Hox* genes in mice and humans. Note how *Hox* gene expression, as indicated with orange, pink, blue, and green shading, occurs in the same body segments in both the mouse and the human. While at least one copy of each Hox gene is present in humans and other vertebrates, some *Hox* genes are missing in some chromosomal sets.



If a *Hox 13* gene in a mouse was replaced with a *Hox 1* gene, how might this alter animal development?

Two of the five clades within the animal kingdom do *not* have *Hox* genes: the Ctenophora and the Porifera. In spite of the superficial similarities

between the Cnidaria and the Ctenophora, the Cnidaria have a number of *Hox* genes, but the Ctenophora have none. The absence of *Hox* genes from the ctenophores has led to the suggestion that they might be “basal” animals, in spite of their tissue differentiation. Ironically, the Placozoa, which have only a few cell types, do have at least one *Hox* gene. The presence of a *Hox* gene in the Placozoa, in addition to similarities in the genomic organization of the Placozoa, Cnidaria and Bilateria, has led to the inclusion of the three groups in a “Parahoxozoa” clade. However, we should note that at this time the reclassification of the Animal Kingdom is still tentative and requires much more study.

Section Summary

Animals constitute an incredibly diverse kingdom of organisms. Although animals range in complexity from simple sea sponges to human beings, most members of the animal kingdom share certain features. Animals are eukaryotic, multicellular, heterotrophic organisms that ingest their food and usually develop into motile creatures with a fixed body plan. A major characteristic unique to the animal kingdom is the presence of differentiated

tissues, such as nerve, muscle, and connective tissues, which are specialized to perform specific functions. Most animals undergo sexual reproduction, leading to a series of developmental embryonic stages that are relatively similar across the animal kingdom. A class of transcriptional control genes called *Hox* genes directs the organization of the major animal body plans, and these genes are strongly homologous across the animal kingdom.

Visual Connection Questions

[link] If a *Hox 13* gene in a mouse was replaced with a *Hox 1* gene, how might this alter animal development?

[link] The animal might develop two heads and no tail.

Review Questions

Which of the following is not a feature common to *most* animals?

1. development into a fixed body plan
2. asexual reproduction
3. specialized tissues
4. heterotrophic nutrient sourcing

B

During embryonic development, unique cell layers develop into specific groups of tissues or organs during a stage called _____.

1. the blastula stage
2. the germ layer stage
3. the gastrula stage
4. the organogenesis stage

C

Which of the following phenotypes would most likely be the result of a *Hox* gene mutation?

1. abnormal body length or height
2. two different eye colors
3. the contraction of a genetic illness
4. two fewer appendages than normal

D

Critical Thinking Questions

Why might the evolution of specialized tissues be important for animal function and complexity?

The development of specialized tissues affords more complex animal anatomy and physiology because differentiated tissue types can perform unique functions and work together in tandem to allow the animal to perform more functions. For example, specialized muscle tissue allows directed and efficient movement, and specialized nervous tissue allows for multiple sensory modalities as well as the ability to respond to various sensory information; these functions are not necessarily available to other nonanimal organisms.

Describe and give examples of how humans display all of the features common to the animal kingdom.

Humans are multicellular organisms. They also contain differentiated tissues, such as epithelial,

muscle, and nervous tissue, as well as specialized organs and organ systems. As heterotrophs, humans cannot produce their own nutrients and must obtain them by ingesting other organisms, such as plants, fungi, and animals. Humans undergo sexual reproduction, as well as the same embryonic developmental stages as other animals, which eventually lead to a fixed and motile body plan controlled in large part by *Hox* genes.

How have *Hox* genes contributed to the diversity of animal body plans?

Altered expression of homeotic genes can lead to major changes in the morphology of the individual. *Hox* genes can affect the spatial arrangements of organs and body parts. If a *Hox* gene was mutated or duplicated, it could affect where a leg might be on a fruit fly or how far apart a person's fingers are.

Glossary

blastula
: 16–32 cell stage of development of an animal embryo

body plan

morphology or defining shape of an organism

cleavage
: cell divisions subdividing a fertilized egg (zygote) to form a multicellular embryo

gastrula
: stage of animal development characterized by the formation of the digestive cavity

germ layer
: collection of cells formed during embryogenesis that will give rise to future body tissues, more pronounced in vertebrate embryogenesis

Hox gene
: (also, homeobox gene) master control gene that can turn on or off large numbers of other genes during embryogenesis

organogenesis
: formation of organs in animal embryogenesis

Sponges and Cnidarians

By the end of this section, you will be able to:

- Describe the organizational features of the simplest animals
- Describe the organizational features of cnidarians

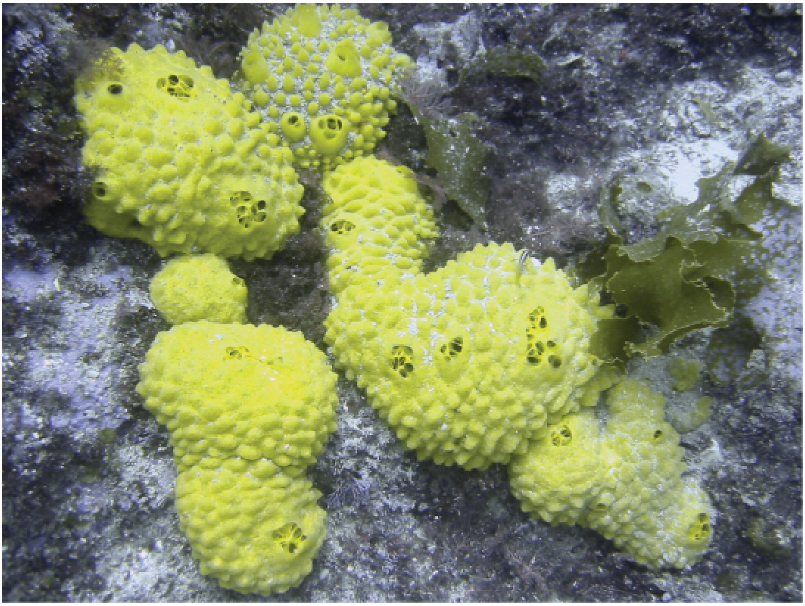
The kingdom of animals is informally divided into invertebrate animals, those without a backbone, and vertebrate animals, those with a backbone. Although in general we are most familiar with vertebrate animals, the vast majority of animal species, about 95 percent, are invertebrates. Invertebrates include a huge diversity of animals, millions of species in about 32 phyla, which we can just begin to touch on here.

The sponges and the cnidarians represent the simplest of animals. Sponges appear to represent an early stage of multicellularity in the animal clade. Although they have specialized cells for particular functions, they lack true tissues in which specialized cells are organized into functional groups. Sponges are similar to what might have been the ancestor of animals: colonial, flagellated protists. The cnidarians, or the jellyfish and their kin, are the simplest animal group that displays true tissues, although they possess only two tissue layers.
Sponges are members of the phylum Porifera, which contains the simplest animals. (credit:

Andrew Turner) The sponge's basic body plan is shown.

Sponges

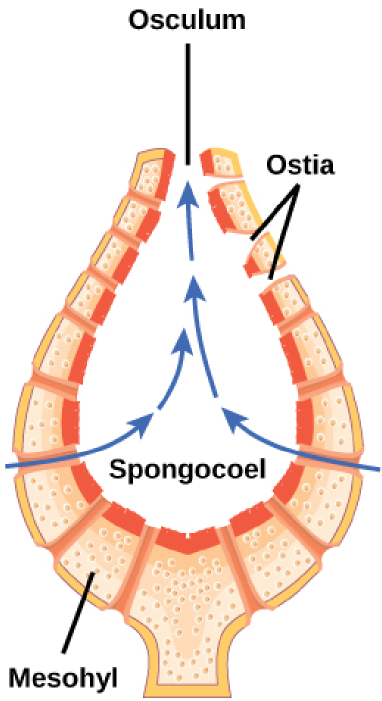
Animals in subkingdom Parazoa represent the simplest animals and include the sponges, or phylum **Porifera** ([link]). All sponges are aquatic and the majority of species are marine. Sponges live in intimate contact with water, which plays a role in their feeding, gas exchange, and excretion. Much of the body structure of the sponge is dedicated to moving water through the body so it can filter out food, absorb dissolved oxygen, and eliminate wastes.



The body of the simplest sponges takes the shape of

a cylinder with a large central cavity, the **spongocoel**. Water enters the spongocoel from numerous pores in the body wall. Water flows out through a large opening called the **osculum** ([link]). However, sponges exhibit a diversity of body forms, which vary in the size and branching of the spongocoel, the number of osculi, and where the cells that filter food from the water are located.

Sponges consist of an outer layer of flattened cells and an inner layer of cells called choanocytes separated by a jelly-like substance called **mesohyl**. The mesohyl contains embedded amoeboid cells that secrete tiny needles called **spicules** or protein fibers that help give the sponge its structural strength. The cell body of the **choanocyte** is embedded in mesohyl but protruding into the spongocoel is a mesh-like collar surrounding a single flagellum. The beating of flagella from all choanocytes moves water through the sponge. Food particles are trapped in mucus produced by the sieve-like collar of the choanocytes and are ingested by phagocytosis. This process is called **intracellular digestion**. **Amoebocytes** take up nutrients repackaged in food vacuoles of the choanocytes and deliver them to other cells within the sponge.



Basic sponge body plan

Physiological Processes in Sponges

Despite their lack of complexity, sponges are clearly successful organisms, having persisted on Earth for more than half a billion years. Lacking a true digestive system, sponges depend on the intracellular digestive processes of their choanocytes for their energy intake. The limit of this type of digestion is that food particles must be smaller than individual cells. Gas exchange, circulation, and excretion occur by diffusion between cells and the water.

Sponges reproduce both sexually and asexually. Asexual reproduction is either by **fragmentation** (in which a piece of the sponge breaks off and develops into a new individual), or **budding** (an outgrowth from the parent that eventually detaches). A type of asexual reproduction found only in freshwater sponges occurs through the formation of **gemmules**, clusters of cells surrounded by a tough outer layer. Gemmules survive hostile environments and can attach to a substrate and grow into a new sponge.

Sponges are **monoecious** (or hermaphroditic), meaning one individual can produce both eggs and sperm. Sponges may be sequentially hermaphroditic, producing eggs first and sperm later. Eggs arise from amoebocytes and are retained within the spongocoel, whereas sperm arise from choanocytes and are ejected through the osculum. Sperm carried by water currents fertilize the eggs of other sponges. Early larval development occurs within the sponge, and free-swimming larvae are then released through the osculum. This is the only time that sponges exhibit mobility. Sponges are sessile as adults and spend their lives attached to a fixed substrate.

Concept in Action

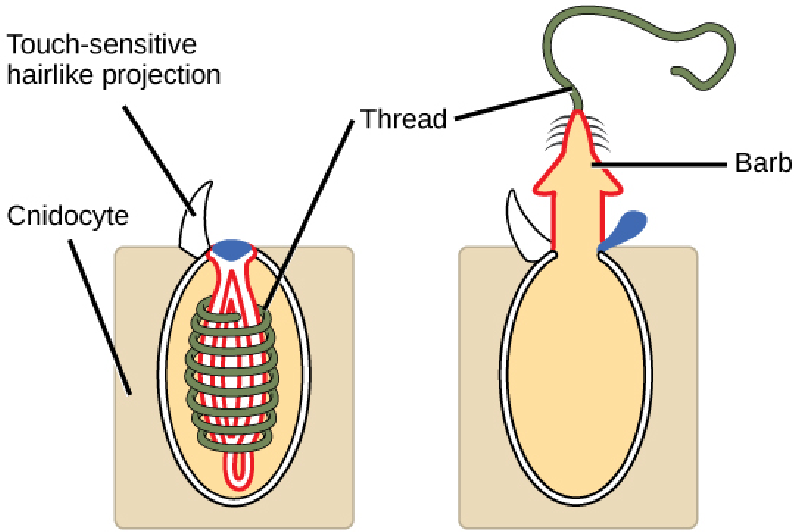
Watch this video that demonstrates the feeding of sponges.

Animals from the phylum Cnidaria have stinging cells called cnidocytes. Cnidocytes contain large organelles called (a) nematocysts that store a coiled thread and barb. When hairlike projections on the cell surface are touched, (b) the thread, barb, and a toxin are fired from the organelle.Cnidarians have two distinct body plans, the (a) medusa and the (b) polyp. All cnidarians have two tissue layers, with a jelly-like mesoglea between them. Sea anemones are cnidarians of class Anthozoa. (credit: "Dancing With Ghosts"/Flickr)Scyphozoans include the jellies. (credit: "Jimg944"/Flickr)“The Hydrozoa Directory,” Peter Schuchert, Muséum Genève, last updated November 2012, http://www.ville-ge.ch/mhng/hydrozoa/hydrozoa-directory.htm.A (a) box jelly is an example from class Cubozoa. The (b) hydra is from class Hydrozoa. (credit b: scale-bar data from Matt Russell)

Cnidarians

The phylum **Cnidaria** includes animals that show radial or biradial symmetry and are diploblastic. Nearly all (about 99 percent) cnidarians are marine species. Cnidarians have specialized cells known as **cnidocytes** (“stinging cells”) containing organelles called **nematocysts**. These cells are concentrated around the mouth and tentacles of the animal and can immobilize prey with toxins. Nematocysts contain coiled threads that may bear barbs. The outer wall of the cell has a hairlike projection that is

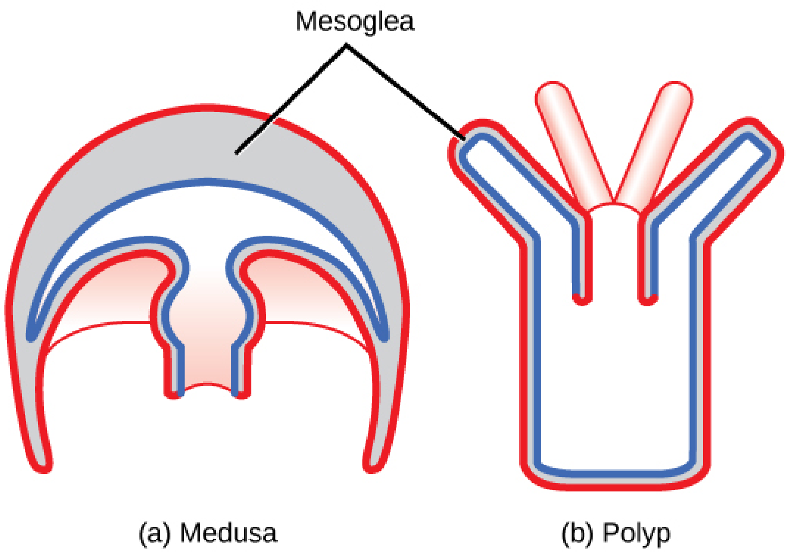
sensitive to touch. When touched, the cells fire the toxin-containing coiled threads that can penetrate and stun the predator or prey (see [link]).



(a) Nematocyst with stored thread and barb

(b) Nematocyst after firing

Cnidarians display two distinct body plans: **polyp** or “stalk” and **medusa** or “bell” ([link]). Examples of the polyp form are freshwater species of the genus *Hydra*; perhaps the best-known medusoid animals are the jellies (jellyfish). Polyps are sessile as adults, with a single opening to the digestive system (the mouth) facing up with tentacles surrounding it. Medusae are motile, with the mouth and tentacles hanging from the bell-shaped body. In other cnidarians, both a polyp and medusa form exist, and the life cycle alternates between these forms.



Physiological Processes of Cnidarians

All cnidarians have two tissue layers. The outer layer is called the **epidermis**, whereas the inner layer is called the **gastrodermis** and lines the digestive cavity. Between these two layers is a non-living, jelly-like **mesoglea**. There are differentiated cell types in each tissue layer, such as nerve cells, enzyme-secreting cells, and nutrient-absorbing cells, as well as intercellular connections between the cells. However, organs and organ systems are not present in this phylum.

The nervous system is primitive, with nerve cells scattered across the body in a network. The function of the nerve cells is to carry signals from sensory cells and to contractile cells. Groups of cells in the nerve net form nerve cords that may be essential for

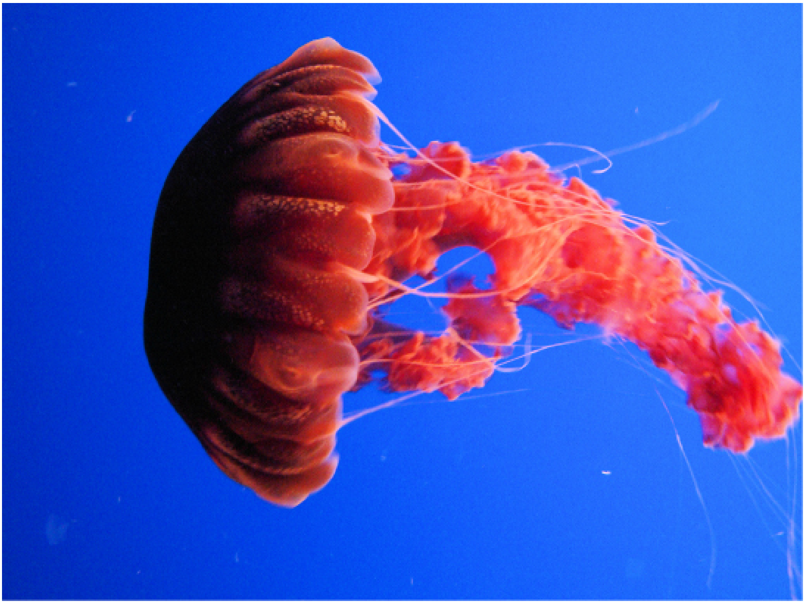
more rapid transmission. Cnidarians perform **extracellular digestion**, with digestion completed by intracellular digestive processes. Food is taken into the **gastrovascular cavity**, enzymes are secreted into the cavity, and the cells lining the cavity absorb the nutrient products of the extracellular digestive process. The gastrovascular cavity has only one opening that serves as both a mouth and an anus (an incomplete digestive system). Like the sponges, Cnidarian cells exchange oxygen, carbon dioxide, and nitrogenous wastes by diffusion between cells in the epidermis and gastrodermis with water.

Cnidarian Diversity

The phylum Cnidaria contains about 10,000 described species divided into four classes: Anthozoa, Scyphozoa, Cubozoa, and Hydrozoa.

The class Anthozoa includes all cnidarians that exhibit a sessile polyp body plan only; in other words, there is no medusa stage within their life cycle. Examples include sea anemones, sea pens, and corals, with an estimated number of 6,100 described species. Sea anemones are usually brightly colored and can attain a size of 1.8 to 10 cm in diameter. These animals are usually cylindrical in shape and are attached to a substrate. A mouth opening is surrounded by tentacles bearing cnidocytes ([link]).

Scyphozoans include all the jellies and are motile and exclusively marine with about 200 described species. The medusa is the dominant stage in the life cycle, although there is also a polyp stage. Species range from 2 cm in length to the largest scyphozoan species, *Cyanea capillata*, at 2 m across. Jellies display a characteristic bell-like body shape ([link]).



Concept in Action
Use this video to identify the life cycle stages of jellies.

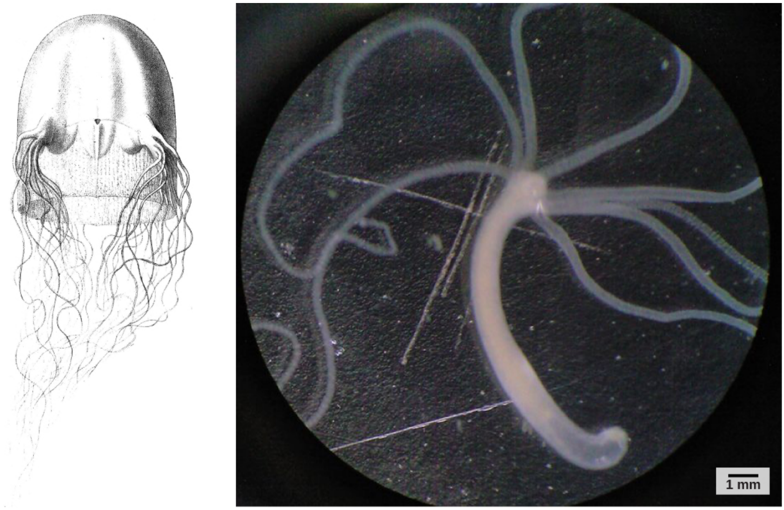
The class Cubozoa includes jellies that are square in cross-section and so are known as “box jellyfish.” These species may achieve sizes of 15–25 cm. Cubozoans are anatomically similar to the jellyfish. A prominent difference between the two classes is the arrangement of tentacles. Cubozoans have muscular pads called pedalia at the corners of the square bell canopy, with one or more tentacles attached to each pedalium. In some cases, the

digestive system may extend into the pedalia. Cubozoans typically exist in a polyp form that develops from a larva. The polyps may bud to form more polyps and then transform into the medusoid forms.

Concept in Action

Watch this video to learn more about the deadly toxins of the box jellyfish.

Hydrozoa includes nearly 3,500 species,[footnote] most of which are marine. Most species in this class have both polyp and medusa forms in their life cycle. Many hydrozoans form colonies composed of branches of specialized polyps that share a gastrovascular cavity. Colonies may also be free-floating and contain both medusa and polyp individuals in the colony, as in the Portuguese Man O'War (*Physalia*) or By-the-Wind Sailor (*Velella*). Other species are solitary polyps or solitary medusae. The characteristic shared by all of these species is that their gonads are derived from epidermal tissue, whereas in all other cnidarians, they are derived from gastrodermal tissue ([link]**ab**).



(a) (b)

Section Summary

Animals included in phylum Porifera are parazoans and do not possess true tissues. These organisms show a simple organization. Sponges have multiple cell types that are geared toward executing various metabolic functions.

Cnidarians have outer and inner tissue layers sandwiching a noncellular mesoglea. Cnidarians possess a well-formed digestive system and carry out extracellular digestion. The cnidocyte is a specialized cell for delivering toxins to prey and predators. Cnidarians have separate sexes. They have a life cycle that involves morphologically distinct forms—medusoid and polypoid—at various stages in their life cycle.

Review Questions

The large central opening in the poriferan body is called the ___.

1. emmule
2. picule
3. stia
4. osculum

D

Cnidocytes are found in ___.

1. phylum Porifera
2. phylum Nemertea
3. phylum Nematoda
4. phylum Cnidaria

D

Cubozoans are _____.

1. polyps

2. medusoids
3. polymorphs
4. sponges

B

Free Response

Describe the feeding mechanism of sponges and identify how it is different from other animals.

The sponges draw water carrying food particles into the spongocoel using the beating of flagella in the choanocytes. The food particles are caught by the collar of the choanocyte and brought into the cell by phagocytosis. Digestion of the food particle takes place inside the cell. The difference between this and the mechanisms of other animals is that digestion takes place within cells rather than outside of cells. It means that the organism can feed only on particles smaller than the cells themselves.

Compare the structural differences between Porifera and Cnidaria.

Poriferans do not possess true tissues, whereas cnidarians do have tissues. Because of this difference, poriferans do not have a nerve net or muscle cells for locomotion, which cnidarians have.

Glossary

amoebocyte
: an amoeba-like cell of sponges whose functions include distribution of nutrients to other cells in the sponge

budding
: a form of asexual reproduction that occurs through the growth of a new organism as a branch on an adult organism that breaks off and becomes independent; found in plants, sponges, cnidarians, and some other invertebrates

choanocyte
: a cell type unique to sponges with a flagellum surrounded by a collar used to maintain water flow through the sponge, and capture and digest food particles

Cnidaria
: a phylum of animals that are diploblastic and have radial symmetry and stinging cells

cnidocyte
: a specialized stinging cell found in Cnidaria

epidermis
: the layer of cells that lines the outer surface of an animal

extracellular digestion
: a form of digestion, the breakdown of food, which occurs outside of cells with the aid of enzymes released by cells

fragmentation
: a form of asexual reproduction in which a portion of the body of an organism breaks off and develops into a living independent organism; found in plants, sponges, and some other invertebrates

gastrodermis
: the layer of cells that lines the gastrovascular cavity of cnidarians

gastrovascular cavity
: the central cavity bounded by the gastrodermis in cnidarians

gemmule
: a structure produced by asexual reproduction in freshwater sponges that is able to survive harsh conditions

intracellular digestion
: the digestion of matter brought into a cell by phagocytosis

medusa
: a free-floating cnidarian body plan with a mouth on the underside and tentacles hanging down from a bell

mesoglea
: the non-living, gel-like matrix present in between ectoderm and endoderm in cnidarians

mesohyl
: the collagen-like gel containing suspended cells that perform various functions in sponges

monoecious
: having both sexes in one body, hermaphroditic

nematocyst
: the harpoon-like organelle within a cnidocyte with a pointed projectile and poison to stun and entangle prey

osculum
: the large opening in a sponge body through which water leaves

polyp
: the stalk-like, sessile life form of a cnidarians with mouth and tentacles facing upward, usually sessile but may be able to glide along a surface

Porifera
: a phylum of animals with no true tissues, but a porous body with a rudimentary endoskeleton

spicule
: a short sliver or spike-like structure, in sponges, they are formed of silicon dioxide, calcium carbonate, or protein, and are found in the mesohyl

spongocoel
: the central cavity within the body of some sponges

Flatworms, Nematodes, and Arthropods

By the end of this section, you will be able to:

- Describe the structure and systems of flatworms
- Describe the structural organization of nematodes
- Compare the internal systems and the appendage specialization of arthropods

The animal phyla of this and subsequent modules are triploblastic and have an embryonic mesoderm sandwiched between the ectoderm and endoderm. These phyla are also bilaterally symmetrical, meaning that a longitudinal section will divide them into right and left sides that are mirror images of each other. Associated with bilateralism is the beginning of cephalization, the evolution of a concentration of nervous tissues and sensory organs in the head of the organism, which is where the organism first encounters its environment.

The flatworms are acoelomate organisms that include free-living and parasitic forms. The nematodes, or roundworms, possess a pseudocoelom and consist of both free-living and parasitic forms. Finally, the arthropods, one of the most successful taxonomic groups on the planet, are coelomate organisms with a hard exoskeleton and jointed appendages. The nematodes and the arthropods belong to a clade with a common ancestor, called Ecdysozoa. The name comes from the word *ecdysis*,

which refers to the periodic shedding, or molting, of the exoskeleton. The ecdysozoan phyla have a hard cuticle covering their bodies that must be periodically shed and replaced for them to increase in size.

This planarian is a free-living flatworm that has an incomplete digestive system, an excretory system with a network of tubules throughout the body, and a nervous system made up of nerve cords running the length of the body with a concentration of nerves and photosensory and chemosensory cells at the anterior end.Phylum Platyhelminthes is divided into four classes: (a) Bedford's Flatworm (*Pseudobiceros bedfordi*) and the (b) planarian belong to class Turbellaria; (c) the Trematoda class includes about 20,000 species, most of which are parasitic; (d) class Cestoda includes tapeworms such as this *Taenia saginata*; and the parasitic class Monogenea (not shown). (credit a: modification of work by Jan Derk; credit c: modification of work by "Sahaquiel9102"/Wikimedia Commons; credit d: modification of work by CDC)

Flatworms

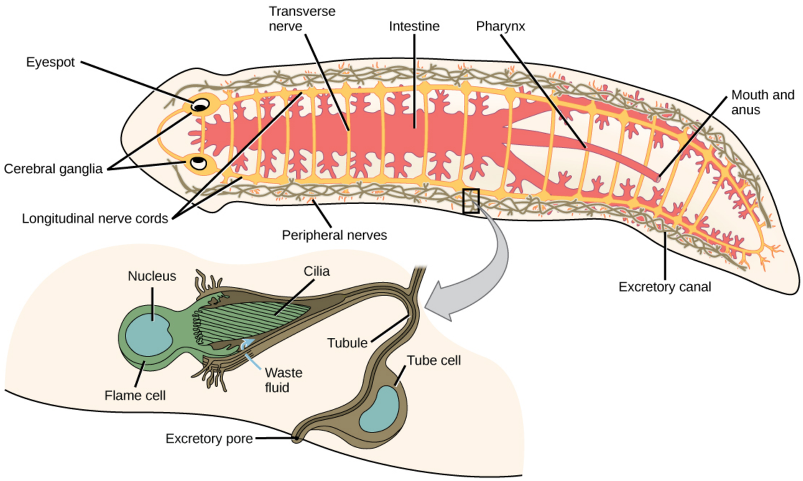
The relationships among flatworms, or phylum Platyhelminthes, is being revised and the description here will follow the traditional groupings. Most flatworms are parasitic, including important parasites of humans. Flatworms have three embryonic germ layers that give rise to

surfaces covering tissues, internal tissues, and the lining of the digestive system. The epidermal tissue is a single layer of cells or a layer of fused cells covering a layer of circular muscle above a layer of longitudinal muscle. The mesodermal tissues include support cells and secretory cells that secrete mucus and other materials to the surface. The flatworms are acoelomate, so their bodies contain no cavities or spaces between the outer surface and the inner digestive tract.

Physiological Processes of Flatworms

Free-living species of flatworms are predators or scavengers, whereas parasitic forms feed from the tissues of their hosts. Most flatworms have an incomplete digestive system with an opening, the "mouth," that is also used to expel digestive system wastes. Some species also have an anal opening. The gut may be a simple sac or highly branched. Digestion is extracellular, with enzymes secreted into the space by cells lining the tract, and digested materials taken into the same cells by phagocytosis. One group, the cestodes, does not have a digestive system, because their parasitic lifestyle and the environment in which they live (suspended within the digestive cavity of their host) allows them to absorb nutrients directly across their body wall. Flatworms have an excretory system with a network of tubules throughout the body that open to the environment and nearby flame cells, whose cilia

beat to direct waste fluids concentrated in the tubules out of the body. The system is responsible for regulation of dissolved salts and excretion of nitrogenous wastes. The nervous system consists of a pair of nerve cords running the length of the body with connections between them and a large ganglion or concentration of nerve cells at the anterior end of the worm; here, there may also be a concentration of photosensory and chemosensory cells ([link]).

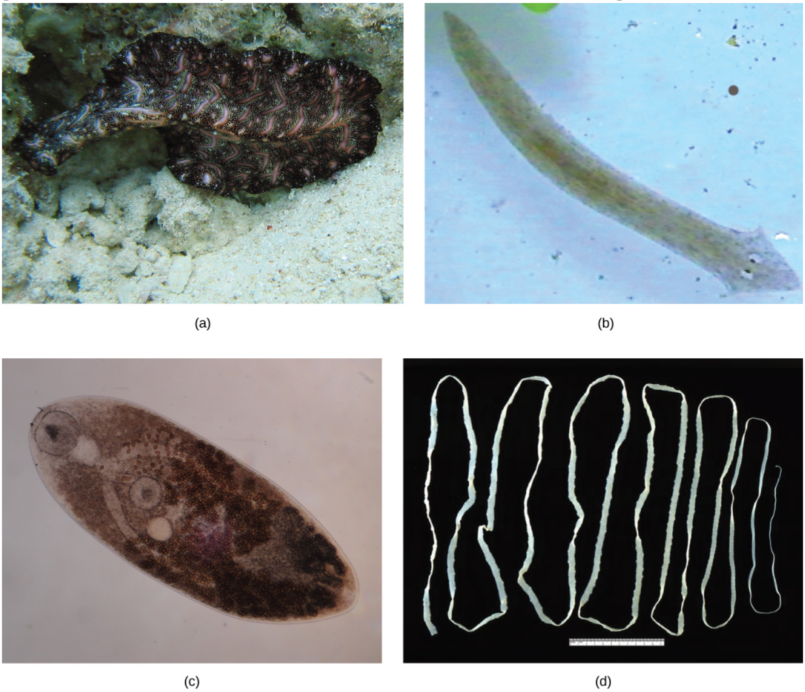


Since there is no circulatory or respiratory system, gas and nutrient exchange is dependent on diffusion and intercellular junctions. This necessarily limits the thickness of the body in these organisms, constraining them to be "flat" worms. Most flatworm species are monoecious (hermaphroditic, possessing both sets of sex organs), and fertilization is typically internal. Asexual reproduction is common in some groups in which an entire organism can be regenerated from just a part of

itself.

Diversity of Flatworms

Flatworms are traditionally divided into four classes: Turbellaria, Monogenea, Trematoda, and Cestoda ([link]). The turbellarians include mainly free-living marine species, although some species live in freshwater or moist terrestrial environments. The simple planarians found in freshwater ponds and aquaria are examples. The epidermal layer of the underside of turbellarians is ciliated, and this helps them move. Some turbellarians are capable of remarkable feats of regeneration in which they may regrow the body, even from a small fragment.



(a) (b) (c) (d)

The monogeneans are external parasites mostly of fish with life cycles consisting of a free-swimming larva that attaches to a fish to begin transformation to the parasitic adult form. They have only one host during their life, typically of just one species. The worms may produce enzymes that digest the host tissues or graze on surface mucus and skin particles. Most monogeneans are hermaphroditic, but the sperm develop first, and it is typical for them to mate between individuals and not to self-fertilize.

The trematodes, or flukes, are internal parasites of mollusks and many other groups, including humans. Trematodes have complex life cycles that involve a primary host in which sexual reproduction occurs and one or more secondary hosts in which asexual reproduction occurs. The primary host is almost always a mollusk. Trematodes are responsible for serious human diseases including schistosomiasis, caused by a blood fluke (*Schistosoma*). The disease infects an estimated 200 million people in the tropics and leads to organ damage and chronic symptoms including fatigue. Infection occurs when a human enters the water, and a larva, released from the primary snail host, locates and penetrates the skin. The parasite infects various organs in the body and feeds on red blood cells before reproducing. Many of the eggs are released in feces and find their way into a waterway where they are able to reinfect the primary snail host.

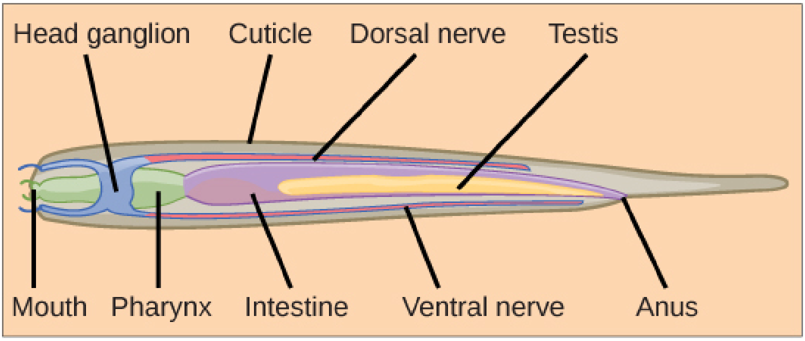
The cestodes, or tapeworms, are also internal parasites, mainly of vertebrates. Tapeworms live in the intestinal tract of the primary host and remain fixed using a sucker on the anterior end, or scolex, of the tapeworm body. The remaining body of the tapeworm is made up of a long series of units called proglottids, each of which may contain an excretory system with flame cells, but will contain reproductive structures, both male and female. Tapeworms do not have a digestive system, they absorb nutrients from the food matter passing them in the host's intestine. Proglottids are produced at the scolex and are pushed to the end of the tapeworm as new proglottids form, at which point, they are "mature" and all structures except fertilized eggs have degenerated. Most reproduction occurs by cross-fertilization. The proglottid detaches and is released in the feces of the host. The fertilized eggs are eaten by an intermediate host. The juvenile worms emerge and infect the intermediate host, taking up residence, usually in muscle tissue. When the muscle tissue is eaten by the primary host, the cycle is completed. There are several tapeworm parasites of humans that are acquired by eating uncooked or poorly cooked pork, beef, and fish.

(a) An scanning electron micrograph of the nematode *Heterodera glycines* and (b) a schematic representation of the anatomy of a nematode are shown. (credit a: modification of work by USDA, ARS; scale-bar data from Matt Russell)

Nematodes

The phylum **Nematoda**, or roundworms, includes more than 28,000 species with an estimated 16,000 parasitic species. The name Nematoda is derived from the Greek word “nemos,” which means “thread.” Nematodes are present in all habitats and are extremely common, although they are usually not visible ([link]).

(a)



(b)

Most nematodes look similar to each other: slender tubes, tapered at each end ([link]). Nematodes are pseudocoelomates and have a **complete digestive system** with a distinct mouth and anus.

The nematode body is encased in a cuticle, a flexible but tough exoskeleton, or external skeleton, which offers protection and support. The cuticle contains a carbohydrate-protein polymer called **chitin**. The cuticle also lines the pharynx and rectum. Although the exoskeleton provides protection, it restricts growth, and therefore must be continually shed and replaced as the animal increases in size.

A nematode's mouth opens at the anterior end with three or six lips and, in some species, teeth in the form of cuticular extensions. There may also be a sharp stylet that can protrude from the mouth to stab prey or pierce plant or animal cells. The mouth leads to a muscular pharynx and intestine, leading to the rectum and anal opening at the posterior end.

Physiological Processes of Nematodes

In nematodes, the excretory system is not specialized. Nitrogenous wastes are removed by diffusion. In marine nematodes, regulation of water and salt is achieved by specialized glands that remove unwanted ions while maintaining internal body fluid concentrations.

Most nematodes have four nerve cords that run along the length of the body on the top, bottom, and sides. The nerve cords fuse in a ring around the pharynx, to form a head ganglion or "brain" of the worm, as well as at the posterior end to form the

tail ganglion. Beneath the epidermis lies a layer of longitudinal muscles that permits only side-to-side, wave-like undulation of the body.

Concept in Action

View this video to see nematodes move about and feed on bacteria.

Nematodes employ a diversity of sexual reproductive strategies depending on the species; they may be monoecious, **dioecious** (separate sexes), or may reproduce asexually by parthenogenesis. *Caenorhabditis elegans* is nearly unique among animals in having both self-fertilizing hermaphrodites and a male sex that can mate with the hermaphrodite.

Trilobites, like the one in this fossil, are an extinct group of arthropods. (credit: Kevin Walsh)The book lungs of (a) arachnids are made up of alternating air pockets and hemocoel tissue shaped like a stack of books. The book gills of (b) crustaceans are similar to book lungs but are external so that gas exchange can occur with the surrounding water. (credit a: modification of work by Ryan Wilson based on original work by John Henry Comstock; credit b: modification of work by Angel Schatz) In this basic anatomy of a hexapod, note that insects have a

developed digestive system (yellow), a respiratory system (blue), a circulatory system (red), and a nervous system (purple).(a) The centipede *Scutigera coleoptrata* has up to 15 pairs of legs. (b) This North American millipede (*Narceus americanus)* bears many legs, although not one thousand, as its name might suggest. (credit a: modification of work by Bruce Marlin; credit b: modification of work by Cory Zanker)“Number of Living Species in Australia and the World,” A.D. Chapman, Australia Biodiversity Information Services, last modified August 26, 2010, http://www.environment.gov.au/biodiversity/abrs/publications/other/species-numbers/2009/03-exec-summary.html. The crayfish is an example of a crustacean. It has a carapace around the cephalothorax and the heart in the dorsal thorax area. (credit: Jane Whitney)“Number of Living Species in Australia and the World,” A.D. Chapman, Australia Biodiversity Information Services, last modified August 26, 2010, http://www.environment.gov.au/biodiversity/abrs/publications/other/species-numbers/2009/03-exec-summary.html. (a) The chelicerae (first set of appendages) are well developed in the Chelicerata, which includes scorpions (a) and spiders (b). (credit a: modification of work by Kevin Walsh; credit b: modification of work by Marshal Hedin)

Arthropoda

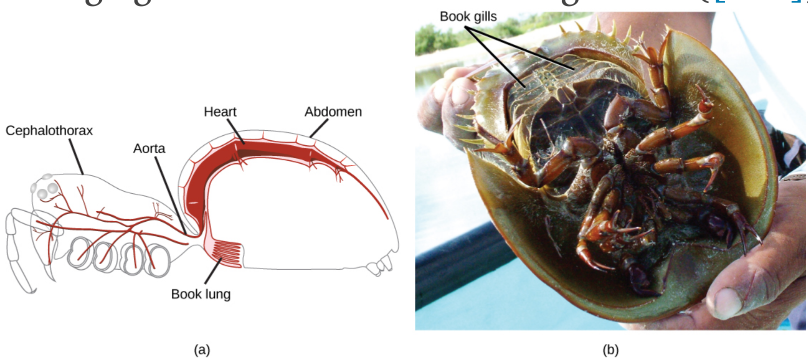
The name “arthropoda” means “jointed legs,” which

aptly describes each of the enormous number of species belonging to this phylum. **Arthropoda** dominate the animal kingdom with an estimated 85 percent of known species, with many still undiscovered or undescribed. The principal characteristics of all the animals in this phylum are functional segmentation of the body and the presence of jointed appendages ([link]). As members of Ecdysozoa, arthropods also have an exoskeleton made principally of chitin. Arthropoda is the largest phylum in the animal world in terms of numbers of species, and insects form the single largest group within this phylum. Arthropods are true coelomate animals and exhibit prostostomic development.

Physiological Processes of Arthropods

A unique feature of arthropods is the presence of a segmented body with fusion of certain sets of segments to give rise to functional segments. Fused

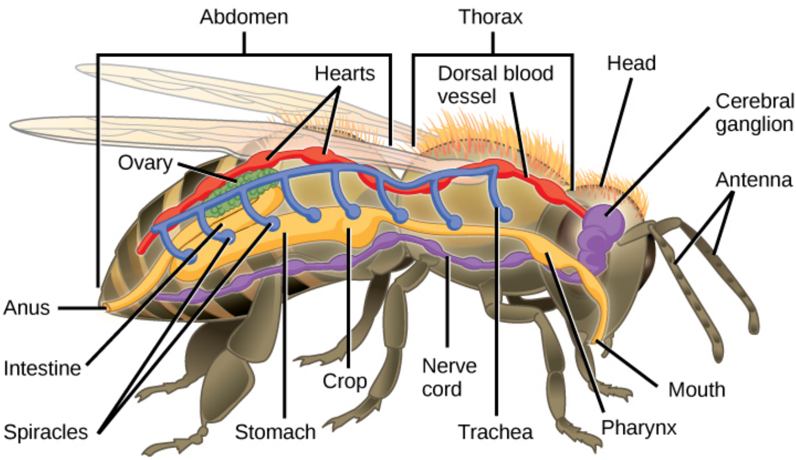
segments may form a head, thorax, and abdomen, or a cephalothorax and abdomen, or a head and trunk. The coelom takes the form of a **hemocoel** (or blood cavity). The open circulatory system, in which blood bathes the internal organs rather than circulating in vessels, is regulated by a two-chambered heart. Respiratory systems vary, depending on the group of arthropod: Insects and myriapods use a series of tubes (**tracheae**) that branch throughout the body, open to the outside through openings called **spiracles**, and perform gas exchange directly between the cells and air in the tracheae. Aquatic crustaceans use gills, arachnids employ "book lungs," and aquatic chelicerates use "book gills." The book lungs of arachnids are internal stacks of alternating air pockets and hemocoel tissue shaped like the pages of a book. The book gills of crustaceans are external structures similar to book lungs with stacks of leaf-like structures that exchange gases with the surrounding water ([link]).



Arthropod Diversity

Phylum Arthropoda includes animals that have been successful in colonizing terrestrial, aquatic, and aerial habitats. The phylum is further classified into five subphyla: Trilobitomorpha (trilobites), Hexapoda (insects and relatives), Myriapoda (millipedes, centipedes, and relatives), Crustacea (crabs, lobsters, crayfish, isopods, barnacles, and some zooplankton), and Chelicerata (horseshoe crabs, arachnids, scorpions, and daddy longlegs). Trilobites are an extinct group of arthropods found from the Cambrian period (540–490 million years ago) until they became extinct in the Permian (300–251 million years ago) that are probably most closely related to the Chelicerata. The 17,000 described species have been identified from fossils ([link]).

The Hexapoda have six legs (three pairs) as their name suggests. Hexapod segments are fused into a head, thorax, and abdomen ([link]). The thorax bears the wings and three pairs of legs. The insects we encounter on a daily basis—such as ants, cockroaches, butterflies, and bees—are examples of Hexapoda.



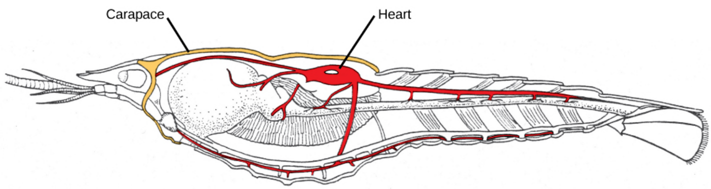
Subphylum Myriapoda includes arthropods with legs that may vary in number from 10 to 750. This subphylum includes 13,000 species; the most commonly found examples are millipedes and centipedes. All myriapods are terrestrial animals and prefer a humid environment ([link]).

(a) (b)

Crustaceans, such as shrimp, lobsters, crabs, and crayfish, are the dominant aquatic arthropods. A few crustaceans are terrestrial species like the pill bugs or sow bugs. The number of described crustacean species stands at about 47,000. [footnote]

Although the basic body plan in crustaceans is

similar to the Hexapoda—head, thorax, and abdomen—the head and thorax may be fused in some species to form a **cephalothorax**, which is covered by a plate called the carapace ([link]). The exoskeleton of many species is also infused with calcium carbonate, which makes it even stronger than in other arthropods. Crustaceans have an open circulatory system in which blood is pumped into the hemocoel by the dorsal heart. Most crustaceans typically have separate sexes, but some, like barnacles, may be hermaphroditic. Serial hermaphroditism, in which the gonad can switch from producing sperm to ova, is also found in some crustacean species. Larval stages are seen in the early development of many crustaceans. Most crustaceans are carnivorous, but detritivores and filter feeders are also common.



Subphylum Chelicerata includes animals such as spiders, scorpions, horseshoe crabs, and sea spiders. This subphylum is predominantly terrestrial, although some marine species also exist. An estimated 103,000[footnote] described species are included in subphylum Chelicerata.

The body of chelicerates may be divided into two parts and a distinct “head” is not always discernible.

The phylum derives its name from the first pair of appendages: the **chelicerae** ([link]**a**), which are specialized mouthparts. The chelicerae are mostly used for feeding, but in spiders, they are typically modified to inject venom into their prey ([link]**b**). As in other members of Arthropoda, chelicerates also utilize an open circulatory system, with a tube-like heart that pumps blood into the large hemocoel that bathes the internal organs. Aquatic chelicerates utilize gill respiration, whereas terrestrial species use either tracheae or book lungs for gaseous exchange.

Concept in Action

Click through this lesson on arthropods to explore interactive habitat maps and more.

Section Summary

Flatworms are acoelomate, triploblastic animals. They lack circulatory and respiratory systems, and have a rudimentary excretory system. The digestive system is incomplete in most species. There are four traditional classes of flatworms, the largely free-living turbellarians, the ectoparasitic monogeneans, and the endoparasitic trematodes and cestodes. Trematodes have complex life cycles involving a secondary mollusk host and a primary host in which sexual reproduction takes place. Cestodes, or tapeworms, infect the digestive systems of primary vertebrate hosts.

Nematodes are pseudocoelomate members of the clade Ecdysozoa. They have a complete digestive system and a pseudocoelomic body cavity. This phylum includes free-living as well as parasitic organisms. They include dioecious and hermaphroditic species. Nematodes have a poorly developed excretory system. Embryonic development is external and proceeds through larval stages separated by molts.

Arthropods represent the most successful phylum of animals on Earth, in terms of number of species as well as the number of individuals. They are characterized by a segmented body and jointed appendages. In the basic body plan, a pair of appendages is present per body segment. Within the phylum, classification is based on mouthparts, number of appendages, and modifications of

appendages. Arthropods bear a chitinous exoskeleton. Gills, tracheae, and book lungs facilitate respiration. Embryonic development may include multiple larval stages.

Review Questions

Which group of flatworms are primarily external parasites of fish?

1. monogeneans
2. trematodes
3. cestodes
4. turbellarians

A

Crustaceans are ____.

1. ecdysozoans
2. nematodes
3. arachnids
4. parazoans

A

Free Response

Speculate as to what advantage(s) a complete digestive system has over an incomplete digestive system?

In a complete digestive system, food material is not mixed with waste material, so the digestion and uptake of nutrients can be more efficient. In addition, the complete digestive system allows for an orderly progression of digestion of food matter and the specialization of different zones of the digestive tract.

Describe a potential advantage and disadvantage of the cuticle of ecdysozoans.

An advantage is that it is a tough covering that is protective against adverse environments, and predators and parasites. A disadvantage is that it must be shed and regrown for the animal to grow, which requires energy and makes the animal vulnerable during this process.

Glossary

Arthropoda
: a phylum of Ecdysozoa with jointed appendages and segmented bodies

cephalothorax
: a fused head and thorax

chelicerae
: a modified first pair of appendages in subphylum Chelicerata

chitin
: a tough nitrogen-containing polysaccharide found in the cuticles of arthropods and the cell walls of fungi

complete digestive system
: a digestive system that opens at one end, the mouth, and exits at the other end, the anus, and through which food normally moves in one direction

dioecious
: having separate male and female sexes

hemocoel
: the internal body cavity seen in arthropods

Nematoda
: a phylum of worms in Ecdysozoa commonly

called roundworms containing both free-living and parasitic forms

spiracle
: a respiratory openings in insects that allow air into the tracheae

trachea
: in some arthropods, such as insects, a respiratory tube that conducts air from the spiracles to the tissues

Mollusks and Annelids
By the end of this section, you will be able to:

- Describe the unique anatomical features of mollusks
- Describe the features of an animal classified in phylum Annelida

The mollusks are a diverse group (85,000 described species) of mostly marine species. They have a variety of forms, ranging from large predatory squid and octopus, some of which show a high degree of intelligence, to small grazing forms with elaborately sculpted and colored shells. The annelids traditionally include the oligochaetes, which include the earthworms and leeches, the polychaetes, which are a marine group, and two other smaller classes.

The phyla Mollusca and Annelida belong to a clade called the **Lophotrochozoa**, which also includes the phylum Nemertea, or ribbon worms ([link]). They are distinct from the Ecdysozoa (nematodes and arthropods) based on evidence from analysis of their DNA, which has changed our views of the relationships among invertebrates.
This chiton from the class Polyplacophora has the eight-plated shell indicative of its class. (credit: Jerry Kirkhart)(a) Like many gastropods, this snail has a stomach foot and a coiled shell. (b) This slug, which is also a gastropod, lacks a shell. (credit a: modification of work by Murray Stevenson; credit b:

modification of work by Rosendahl)The (a) nautilus, (b) giant cuttlefish, (c) reef squid, and (d) blue-ring octopus are all members of the class Cephalopoda. (credit a: modification of work by J. Baecker; credit b: modification of work by Adrian Mohedano; credit c: modification of work by Silke Baron; credit d: modification of work by Angell Williams) *Antalis vulgaris* shows the classic Dentaliidae shape that gives these animals their common name of "tusk shell." (credit: Georges Jansoone)

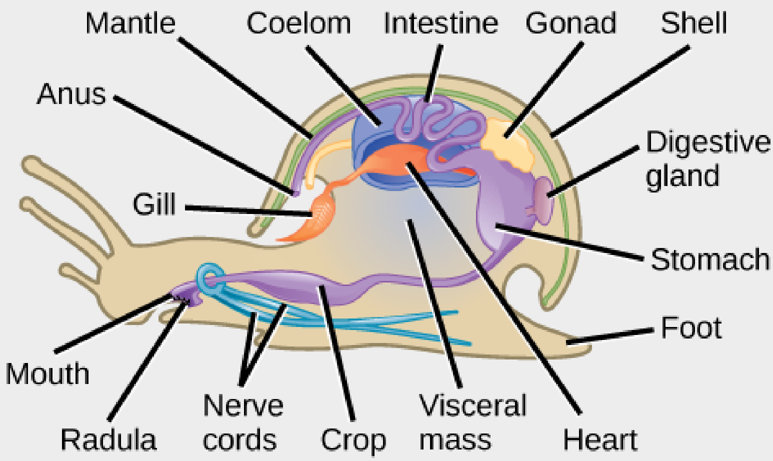
Phylum Mollusca

Mollusca is the predominant phylum in marine environments, where it is estimated that 23 percent of all known marine species belong to this phylum. It is the second most diverse phylum of animals with over 75,000 described species. The name "mollusca" signifies a soft body, as the earliest descriptions of mollusks came from observations of unshelled, soft-bodied cuttlefish (squid relatives). Although mollusk body forms vary, they share key characteristics, such as a ventral, muscular foot that is typically used for locomotion; the visceral mass, which contains most of the internal organs of the animal; and a dorsal mantle, which is a flap of tissue over the visceral mass that creates a space called the mantle cavity. The mantle may or may not secrete a shell of calcium carbonate. In addition, many mollusks have a scraping structure at the mouth, called a **radula** ([link]).

The muscular foot varies in shape and function, depending on the type of mollusk (described below in the section on mollusk diversity). It is a retractable as well as extendable organ, used for locomotion and anchorage. Mollusks are eucoelomates, but the coelomic cavity is restricted to a cavity around the heart in adult animals. The mantle cavity, formed inside the **mantle**, develops independently of the coelomic cavity. It is a multi-purpose space, housing the gills, the anus, organs for sensing food particles in the water, and an outlet for gametes. Most mollusks have an open circulatory system with a heart that circulates the hemolymph in open spaces around the organs. The octopuses and squid are an exception to this and have a closed circulatory system with two hearts that move blood through the gills and a third, systemic heart that pumps blood through the rest of the body.

Visual Connection

There are many species and variations of mollusks; the gastropod mollusk anatomy is shown here, which shares many characteristics common with other groups.



Which of the following statements about the anatomy of a mollusk is false?

1. Mollusks have a radula for scraping food.
2. Mollusks have ventral nerve cords.
3. The tissue beneath the shell is called the mantle.
4. The mantle cavity contains hemolymph.

Mollusk Diversity

This phylum is comprised of seven classes: Aplacophora, Monoplacophora, Polyplacophora, Bivalvia, Gastropoda, Cephalopoda, and Scaphopoda.

Class Aplacophora ("bearing no plates") includes worm-like animals living mostly on deep ocean bottoms. These animals lack a shell but have

aragonite spicules on their skin. Members of class Monoplacophora (“bearing one plate”) have a single, cap-like shell enclosing the body. The monoplacophorans were believed extinct and only known as fossils until the discovery of *Neopilina galatheae* in 1952. Today, scientists have identified nearly two dozen living species.

Animals in the class Polyplacophora (“bearing many plates”) are commonly known as “chitons” and bear an armor-like, eight-plated shell ([link]). These animals have a broad, ventral foot that is adapted for attachment to rocks and a mantle that extends beyond the shell in the form of a girdle. They breathe with **ctenidia** (gills) present ventrally. These animals have a radula modified for scraping. A single pair of nephridia for excretion is present.

Class Bivalvia (“two shells”) includes clams, oysters, mussels, scallops, and geoducks. They are found in

marine and freshwater habitats. As the name suggests, bivalves are enclosed in a pair of shells (or valves) that are hinged at the dorsal side. The body is flattened on the sides. They feed by filtering particles from water and a radula is absent. They exchange gases using a pair of ctenidia, and excretion and osmoregulation are carried out by a pair of nephridia. In some species, the posterior edges of the mantle may fuse to form two siphons that inhale and exhale water. Some bivalves like oysters and mussels have the unique ability to secrete and deposit a calcareous **nacre** or "mother of pearl" around foreign particles that enter the mantle cavity. This property is commercially exploited to produce pearls.

Concept in Action
Watch animations of clams and mussels feeding to understand more about bivalves.

Gastropods ("stomach foot") include well-known mollusks like snails, slugs, conchs, sea hares, and sea butterflies. Gastropods include shell-bearing species as well as species with a reduced shell. These animals are asymmetrical and usually present a coiled shell ([link]).

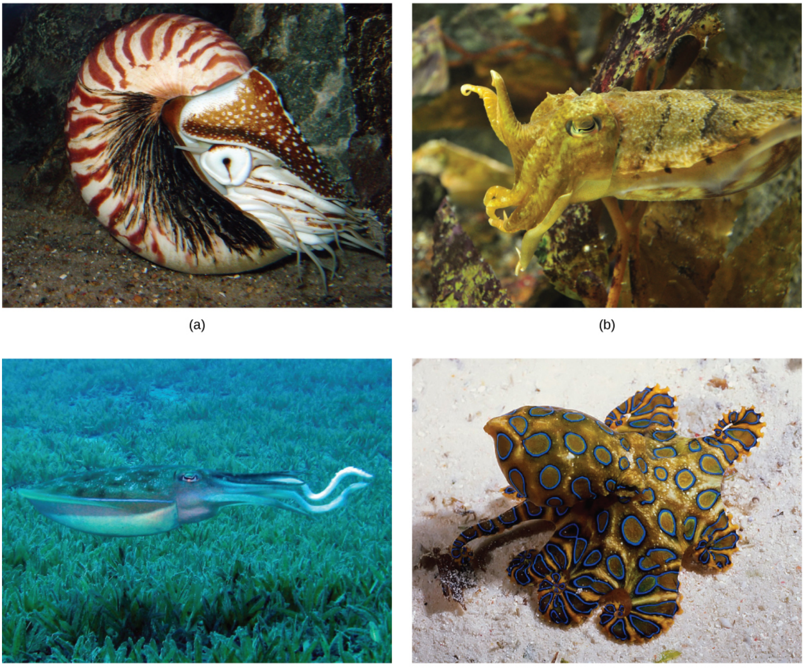
(a) (b)

The visceral mass in the shelled species is characteristically twisted and the foot is modified for crawling. Most gastropods bear a head with tentacles that support eyes. A complex radula is used to scrape food particles from the substrate. The mantle cavity encloses the ctenidia as well as a pair of nephridia.

The class Cephalopoda (“head foot” animals) includes octopuses, squids, cuttlefish, and nautilus. Cephalopods include shelled and reduced-shell groups. They display vivid coloration, typically seen in squids and octopuses, which is used for camouflage. The ability of some octopuses to rapidly adjust their colors to mimic a background pattern or to startle a predator is one of the more awe-inspiring feats of these animals. All animals in this class are predators and have beak-like jaws. All cephalopods have a well-developed nervous system, complex eyes, and a closed circulatory system. The foot is lobed and developed into tentacles and a funnel, which is used for locomotion. Suckers are present on the tentacles in octopuses and squid.

Ctenidia are enclosed in a large mantle cavity and are serviced by large blood vessels, each with its own heart.

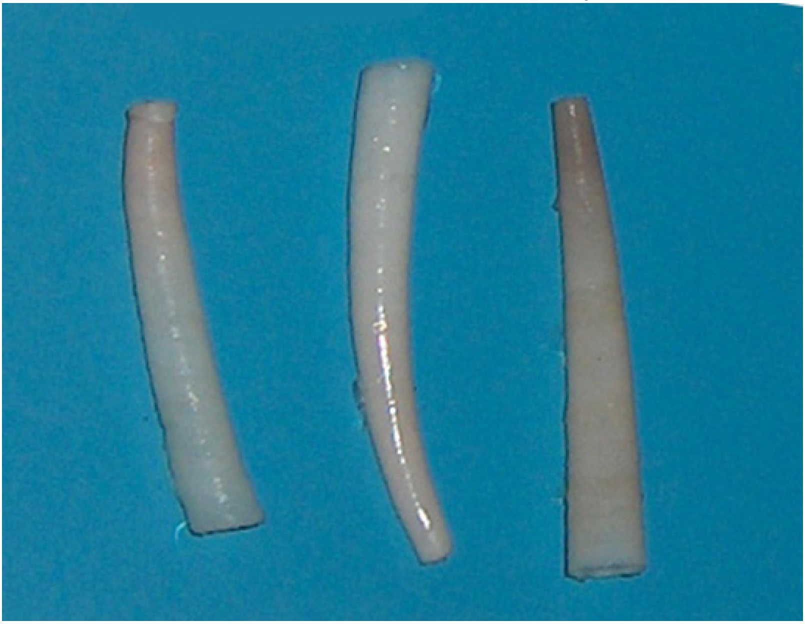
Cephalopods ([link]) are able to move quickly via jet propulsion by contracting the mantle cavity to forcefully eject a stream of water. Cephalopods have separate sexes, and the females of some species care for the eggs for an extended period of time. Although the shell is much reduced and internal in squid and cuttlefish, and absent altogether in octopus, nautilus live inside a spiral, multi-chambered shell that is filled with gas or water to regulate buoyancy.



(a) (b) (c) (d)

Members of the class Scaphopoda ("boat feet") are

known colloquially as “tusk shells” or “tooth shells.” Tooth shells are open at both ends and usually lie buried in sand with the front opening exposed to water and the reduced head end projecting from the back of the shell. Tooth shells have a radula and a foot modified into tentacles, each with a bulbous end that catches and manipulates prey ([link]).



Annelida

Phylum **Annelida** are segmented worms found in marine, terrestrial, and freshwater habitats, but the presence of water or humidity is a critical factor for their survival in terrestrial habitats. The name of the phylum is derived from the Latin word *annellus*, which means a small ring. Approximately 16,500

species have been described. The phylum includes earthworms, polychaete worms, and leeches. Like mollusks, annelids exhibit protostomic development.

Annelids are bilaterally symmetrical and have a worm-like appearance. Their particular segmented body plan results in repetition of internal and external features in each body segment. This type of body plan is called **metamerism**. The evolutionary benefit of such a body plan is thought to be the capacity it allows for the evolution of independent modifications in different segments that perform different functions. The overall body can then be divided into head, body, and tail.

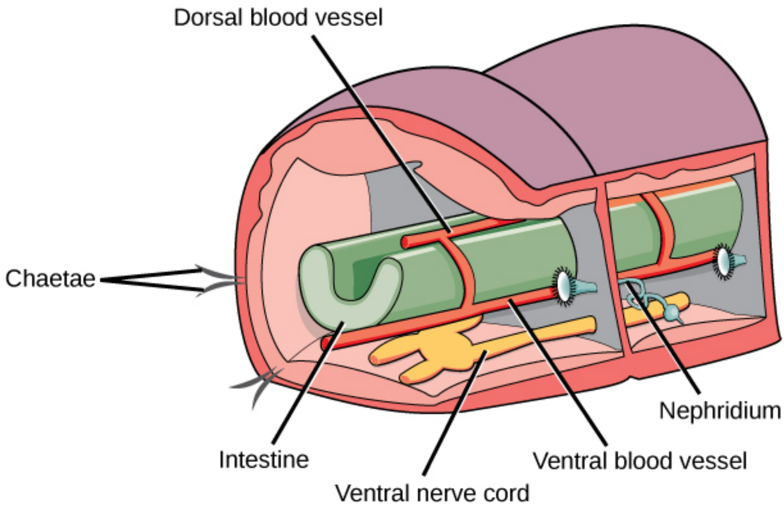
In this schematic showing the basic anatomy of annelids, the digestive system is indicated in green, the nervous system is indicated in yellow, and the circulatory system is indicated in red.

Physiological Processes of Annelida

The skin of annelids is protected by a cuticle that is thinner than the cuticle of the ecdysozoans and does not need to be molted for growth. Chitinous hairlike extensions, anchored in the skin and projecting from the cuticle, called **chaetae**, are present in every segment in most groups. The chaetae are a defining character of annelids. Polychaete worms have paired, unjointed limbs called parapodia on each segment used for locomotion and breathing. Beneath the cuticle there are two layers of muscle,

one running around its circumference (circular) and one running the length of the worm (longitudinal). Annelids have a true coelom in which organs are distributed and bathed in coelomic fluid. Annelids possess a well-developed complete digestive system with specialized organs: mouth, muscular pharynx, esophagus, and crop. A cross-sectional view of a body segment of an earthworm is shown in [link]; each segment is limited by a membrane that divides the body cavity into compartments.

Annelids have a closed circulatory system with muscular pumping “hearts” in the anterior segments, dorsal and ventral blood vessels that run the length of the body with connections in each segment, and capillaries that service individual tissues. Gas exchange occurs across the moist body surface. Excretion is carried out by pairs of primitive “kidneys” called metanephridia that consist of a convoluted tubule and an open, ciliated funnel present in every segment. Annelids have a well-developed nervous system with two ventral nerve cords and a nerve ring of fused ganglia present around the pharynx.



Annelids may be either monoecious with permanent gonads (as in earthworms and leeches) or dioecious with temporary or seasonal gonads (as in polychaetes).

Concept in Action
This video and animation provides a close-up look at annelid anatomy.

The (a) earthworm and (b) leech are both annelids. (credit a: modification of work by "schizoform"/ Flickr; credit b: modification of work by "Sarah G…"/Flickr)

Annelid Diversity

Phylum Annelida includes the classes Polychaeta and Clitellata ([link]); the latter contains subclasses Oligochaeta, Hirudinoidea, and Branchiobdellida.

Earthworms are the most abundant members of the subclass Oligochaeta, distinguished by the presence of the **clitellum**, a ring structure in the skin that secretes mucus to bind mating individuals and forms a protective cocoon for the eggs. They also have a few, reduced chaetae (oligo- = "few"; -chaetae = "hairs"). The number and size of chaetae is greatly diminished in oligochaetes as compared to the polychaetes (poly- = "many"; -chaetae = "hairs"). The chaetae of polychaetes are also arranged within fleshy, flat, paired appendages on each segment called parapodia.

The subclass Hirudinoidea includes leeches. Significant differences between leeches and other annelids include the development of suckers at the anterior and posterior ends, and the absence of chaetae. Additionally, the segmentation of the body wall may not correspond to internal segmentation of the coelomic cavity. This adaptation may allow leeches to swell when ingesting blood from host vertebrates. The subclass Branchiobdellida includes about 150 species that show similarity to leeches as well as oligochaetes. All species are obligate symbionts, meaning that they can only survive

associated with their host, mainly with freshwater crayfish. They feed on the algae that grows on the carapace of the crayfish.

(a) (b)

Section Summary

The phylum Mollusca is a large, mainly marine group of invertebrates. Mollusks show a variety of morphologies. Many mollusks secrete a calcareous shell for protection, but in other species, the shell is reduced or absent. Mollusks are protostomes. The dorsal epidermis in mollusks is modified to form the mantle, which encloses the mantle cavity and visceral organs. This cavity is distinct from the coelomic cavity, which the adult animal retains, surrounding the heart. Respiration is facilitated by gills known as ctenidia. A chitinous scraper called the radula is present in most mollusks. Mollusks are mostly dioecious and are divided into seven classes.

The phylum Annelida includes worm-like, segmented animals. Segmentation is both external and internal, which is called metamerism. Annelids

are protostomes. The presence of chitinous hairs called chaetae is characteristic of most members. These animals have well-developed nervous and digestive systems. Polychaete annelids have parapodia that participate in locomotion and respiration. Suckers are seen in the order Hirudinea. Breeding systems include separate sexes and hermaphroditism.

Art Connections

[link] Which of the following statements about the anatomy of a mollusk is false?

1. Mollusks have a radula for scraping food.
2. Mollusks have ventral nerve cords.
3. The tissue beneath the shell is called the mantle.
4. The mantle cavity contains hemolymph.

[link] D

Review Questions

A mantle and mantle cavity are present in ____.

1. class Oligochaeta
2. class Bivalvia
3. class Polychaeta
4. class Hirudinea

C

Annelids have a ____.

1. pseudocoelom
2. a true coelom
3. no coelom
4. none of the above

B

Free Response

Describe the morphology and anatomy of mollusks.

Mollusks have a large muscular foot that may be modified in various ways, such as into

tentacles, but it functions in locomotion. They have a mantle, a structure of tissue that covers and encloses the dorsal portion of the animal and secretes the shell when it is present. The mantle encloses the mantle cavity, which houses the gills (when present), excretory pores, anus, and gonadopores. The coelom of mollusks is restricted to the region around the systemic heart. The main body cavity is a hemocoel. Many mollusks have a radula near the mouth that is used for scraping food.

Glossary

Annelida
: a phylum of worm-like animals with metamerism

chaeta
: a chitinous projection from the cuticle found in annelids

clitellum
: a specialized band of fused segments in some annelids, which aids in reproduction

ctenidia
: specialized gills in mollusks

Lophotrochozoa
: a clade of invertebrate organisms that is a

sister group to the Ecdysozoa

mantle
a specialized epidermis that encloses all visceral organs and secretes shells in mollusks

metamerism
having a series of body structures that are similar internally and externally, such as segments

Mollusca
a phylum of protostomes with soft bodies and no segmentation

nacre
a calcareous secretion produced by bivalve mollusks to line the inner side of shells as well as to coat foreign particulate matter

radula
a tongue-like scraping organ with chitinous ornamentation found in most mollusks

Echinoderms and Chordates
By the end of this section, you will be able to:

- Describe the distinguishing characteristics of echinoderms
- Describe the distinguishing characteristics of chordates

Deuterostomes include the phyla Echinodermata and Chordata (which includes the vertebrates) and two smaller phyla. Deuterostomes share similar patterns of early development.
“Number of Living Species in Australia and the World,” A.D. Chapman, Australia Biodiversity Information Services, last modified August 26, 2010, http://www.environment.gov.au/biodiversity/abrs/publications/other/species-numbers/2009/03-exec-summary.html.

Echinoderms

Echinodermata are named for their spiny skin (from the Greek “echinos” meaning “spiny” and “dermos” meaning “skin”). The phylum includes about 7,000[footnote] described living species, such as sea stars, sea cucumbers, sea urchins, sand dollars, and brittle stars. **Echinodermata** are exclusively marine.

Adult echinoderms exhibit pentaradial symmetry and have a calcareous endoskeleton made of ossicles

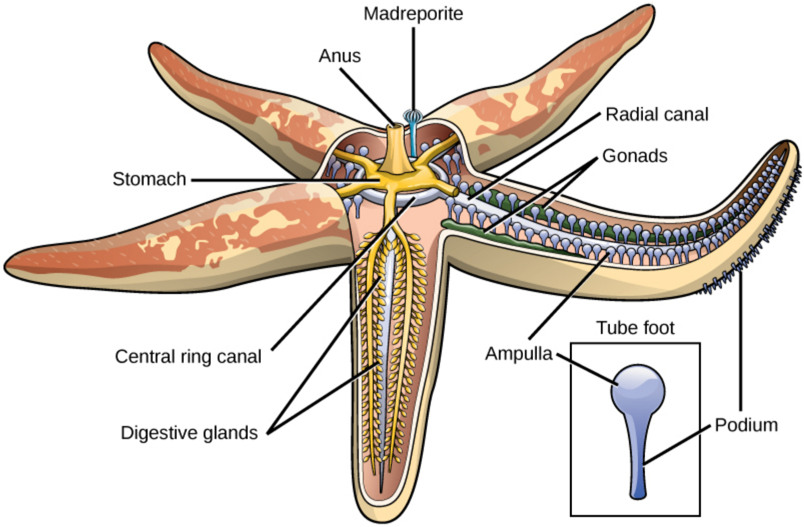
([link]), although the early larval stages of all echinoderms have bilateral symmetry. The endoskeleton is developed by epidermal cells, which may also possess pigment cells, giving vivid colors to these animals, as well as cells laden with toxins. These animals have a true coelom, a portion of which is modified into a unique circulatory system called a **water vascular system**. An interesting feature of these animals is their power to regenerate, even when over 75 percent of their body mass is lost.

This diagram shows the anatomy of a sea star.

Physiological Processes of Echinoderms

Echinoderms have a unique system for gas exchange, nutrient circulation, and locomotion called the water vascular system. The system consists of a central ring canal and radial canals extending along each arm. Water circulates through these structures allowing for gas, nutrient, and waste exchange. A structure on top of the body, called the **madreporite**, regulates the amount of water in the water vascular system. “Tube feet,” which protrude through openings in the endoskeleton, may be expanded or contracted using the hydrostatic pressure in the system. The system allows for slow movement, but a great deal of power, as witnessed when the tube feet latch on to opposite halves of a bivalve mollusk, like a clam, and slowly, but surely pull the shells apart, exposing

the flesh within.



The echinoderm nervous system has a nerve ring at the center and five radial nerves extending outward along the arms. There is no centralized nervous control. Echinoderms have separate sexes and release their gametes into the water where fertilization takes place. Echinoderms may also reproduce asexually through regeneration from body parts.

Different members of Echinodermata include the (a) sea star in class Asteroidea, (b) the brittle star in class Ophiuroidea, (c) the sea urchins of class Echinoidea, (d) the sea lilies belonging to class Crinoidea, and (e) sea cucumbers representing class Holothuroidea. (credit a: modification of work by Adrian Pingstone; credit b: modification of work by Joshua Ganderson; credit c: modification of work by Samuel Chow; credit d: modification of work by Sarah Depper; credit e: modification of work by Ed

Bierman)

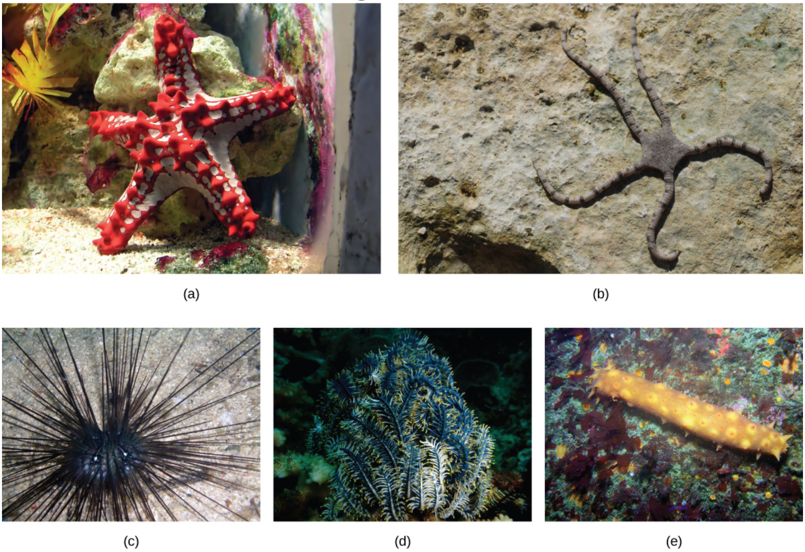
Echinoderm Diversity

This phylum is divided into five classes: Asteroidea (sea stars), Ophiuroidea (brittle stars), Echinoidea (sea urchins and sand dollars), Crinoidea (sea lilies or feather stars), and Holothuroidea (sea cucumbers) ([link]).

Perhaps the best-known echinoderms are members of the class Asteroidea, or sea stars. They come in a large variety of shapes, colors, and sizes, with more than 1,800 species known. The characteristics of sea stars that set them apart from other echinoderm classes include thick arms that extend from a central disk where organs penetrate into the arms. Sea stars use their tube feet not only for gripping surfaces but also for grasping prey. Sea stars have two stomachs, one of which they can evert through their mouths to secrete digestive juices into or onto prey before ingestion. This process can essentially liquefy the prey and make digestion easier.

Concept in Action
View this video to explore a sea star's body plan up close, watch one move across the sea floor, and see it devour a mussel.

Brittle stars have long, thin arms that do not contain any organs. Sea urchins and sand dollars do not have arms but are hemispherical or flattened with five rows of tube feet, which help them in slow movement. Sea lilies and feather stars are stalked suspension feeders. Sea cucumbers are soft-bodied and elongate with five rows of tube feet and a series of tube feet around the mouth that are modified into tentacles used in feeding.



Chordates

The majority of species in the phylum Chordata are found in the subphylum Vertebrata, which include many species with which we are familiar. The vertebrates contain more than 60,000 described species, divided into major groupings of the lampreys, fishes, amphibians, reptiles, birds, and

mammals.

Animals in the phylum **Chordata** share four key features that appear at some stage of their development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail ([link]). In certain groups, some of these traits are present only during embryonic development.

The chordates are named for the **notochord**, which is a flexible, rod-shaped structure that is found in the embryonic stage of all chordates and in the adult stage of some chordate species. It is located between the digestive tube and the nerve cord, and provides skeletal support through the length of the body. In some chordates, the notochord acts as the primary axial support of the body throughout the animal's lifetime. In vertebrates, the notochord is present during embryonic development, at which time it induces the development of the neural tube and serves as a support for the developing embryonic body. The notochord, however, is not found in the postnatal stage of vertebrates; at this point, it has been replaced by the **vertebral column** (the spine).

The **dorsal hollow nerve cord** is derived from ectoderm that sinks below the surface of the skin and rolls into a hollow tube during development. In chordates, it is located dorsally to the notochord. In contrast, other animal phyla possess solid nerve

cords that are located either ventrally or laterally. The nerve cord found in most chordate embryos develops into the brain and spinal cord, which compose the central nervous system.

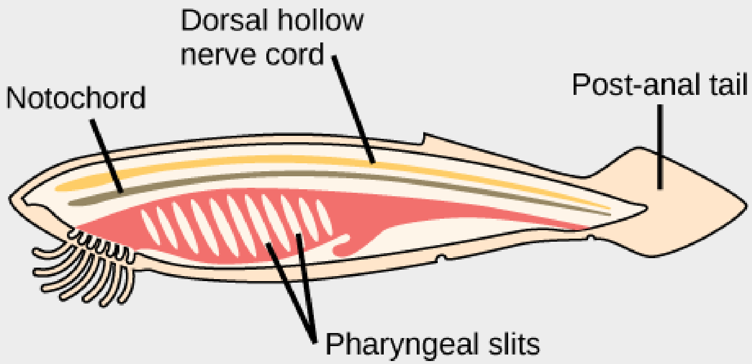
Pharyngeal slits are openings in the pharynx, the region just posterior to the mouth, that extend to the outside environment. In organisms that live in aquatic environments, pharyngeal slits allow for the exit of water that enters the mouth during feeding. Some invertebrate chordates use the pharyngeal slits to filter food from the water that enters the mouth. In fishes, the pharyngeal slits are modified into gill supports, and in jawed fishes, jaw supports. In tetrapods, the slits are further modified into components of the ear and tonsils, since there is no longer any need for gill supports in these air-breathing animals. ***Tetrapod*** means "four-footed," and this group includes amphibians, reptiles, birds, and mammals. (Birds are considered tetrapods because they evolved from tetrapod ancestors.)

The **post-anal tail** is a posterior elongation of the body extending beyond the anus. The tail contains skeletal elements and muscles, which provide a source of locomotion in aquatic species, such as fishes. In some terrestrial vertebrates, the tail may also function in balance, locomotion, courting, and signaling when danger is near. In many species, the tail is absent or reduced; for example, in apes, including humans, it is present in the embryo, but

reduced in size and nonfunctional in adults.

Visual Connection

In chordates, four common features appear at some point in development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. The anatomy of a cephalochordate shown here illustrates all of these features.



Which of the following statements about common features of chordates is true?

1. The dorsal hollow nerve cord is part of the chordate central nervous system.
2. In vertebrate fishes, the pharyngeal slits become the gills.
3. Humans are not chordates because humans do not have a tail.
4. Vertebrates do not have a notochord at any point in their development; instead, they have a vertebral column.

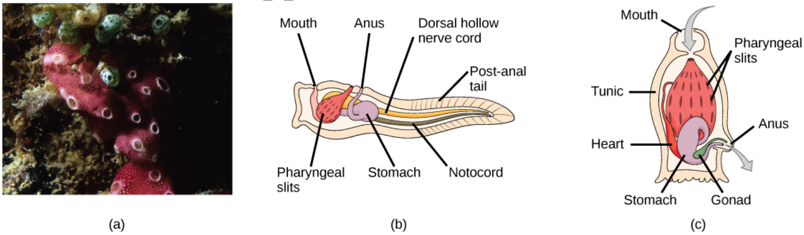
(a) This photograph shows a colony of the tunicate *Botrylloides violaceus*. In the (b) larval stage, the tunicate can swim freely until it attaches to a substrate to become (c) an adult. (credit a: modification of work by Dr. Dwayne Meadows, NOAA/NMFS/OPR) Adult lancelets retain the four key features of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail.

Invertebrate Chordates

In addition to the vertebrates, the phylum Chordata contains two clades of invertebrates: **Urochordata** (tunicates) and **Cephalochordata** (lancelets). Members of these groups possess the four distinctive features of chordates at some point during their development.

The **tunicates** ([link]) are also called sea squirts. The name tunicate derives from the cellulose-like carbohydrate material, called the tunic, which covers the outer body. Although tunicates are classified as chordates, the adult forms are much modified in body plan and do not have a notochord, a dorsal hollow nerve cord, or a post-anal tail, although they do have pharyngeal slits. The larval form possesses all four structures. Most tunicates are hermaphrodites. Tunicate larvae hatch from eggs inside the adult tunicate’s body. After hatching, a tunicate larva swims for a few days until it finds a

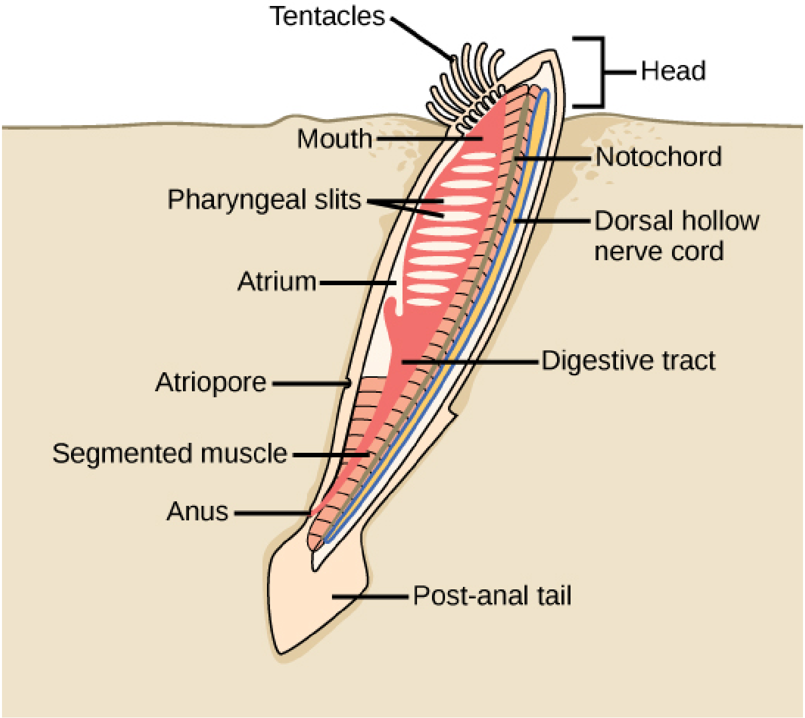
suitable surface on which it can attach, usually in a dark or shaded location. It then attaches by the head to the substrate and undergoes metamorphosis into the adult form, at which point the notochord, nerve cord, and tail disappear.



Most tunicates live a sessile existence in shallow ocean waters and are suspension feeders. The primary foods of tunicates are plankton and detritus. Seawater enters the tunicate's body through its incurrent siphon. Suspended material is filtered out of this water by a mucus net (pharyngeal slits) and is passed into the intestine through the action of cilia. The anus empties into the excurrent siphon, which expels wastes and water.

Lancelets possess a notochord, dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail in the adult stage ([link]). The notochord extends into the head, which gives the subphylum its name (Cephalochordata). Extinct fossils of this subphylum date to the middle of the Cambrian period (540–488 mya).The living forms, the lancelets, are named for their blade-like shape. Lancelets are only a few centimeters long and are usually found buried in

sand at the bottom of warm temperate and tropical seas. Like tunicates, they are suspension feeders.



Section Summary

Echinoderms are deuterostome marine organisms. This phylum of animals bear a calcareous endoskeleton composed of ossicles covered by a spiny skin. Echinoderms possess a water-based circulatory system. The madreporite is the point of entry and exit for water for the water vascular system.

The characteristic features of Chordata are a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Chordata contains two clades of invertebrates: Urochordata (tunicates) and Cephalochordata (lancelets), together with the vertebrates. Most tunicates live on the ocean floor and are suspension feeders. Lancelets are suspension feeders that feed on phytoplankton and other microorganisms.

Art Connections

[link] Which of the following statements about common features of chordates is true?

1. The dorsal hollow nerve cord is part of the chordate central nervous system.
2. In vertebrate fishes, the pharyngeal slits become the gills.
3. Humans are not chordates because humans do not have a tail.
4. Vertebrates do not have a notochord at any point in their development; instead, they have a vertebral column.

[link] A

Review Questions

Echinoderms in their larval state have ___.

1. triangular symmetry
2. radial symmetry
3. hexagonal symmetry
4. bilateral symmetry

D

The circulatory fluid in echinoderms is ___.

1. blood
2. mesohyl
3. water
4. saline

C

Which of the following is *not* a member of the phylum Chordata?

1. Cephalochordata
2. Echinodermata
3. Urochordata
4. Vertebrata

B

Free Response

Sessile adult tunicates lose the notochord; what does this suggest about one function of this structure?

It suggests that the notochord is important for support during locomotion of an organism.

During embryonic development, what features do we share with tunicates or lancelets?

During embryonic development, we also have a notochord, a dorsal hollow nerve tube, pharyngeal slits, and a post-anal tail.

Glossary

Cephalochordata
: a chordate clade whose members possess a notochord, dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail in the

adult stage

Chordata
: a phylum of animals distinguished by their possession of a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail at some point during their development

dorsal hollow nerve cord
: a hollow, tubular structure derived from ectoderm, which is located dorsal to the notochord in chordates

Echinodermata
: a phylum of deuterostomes with spiny skin; exclusively marine organisms

lancelet
: a member of Cephalochordata; named for its blade-like shape

madreporite
: a pore for regulating entry and exit of water into the water vascular system

notochord
: a flexible, rod-shaped structure that is found in the embryonic stage of all chordates and in the adult stage of some chordates

pharyngeal slit
: an opening in the pharynx

post-anal tail
: a muscular, posterior elongation of the body extending beyond the anus in chordates

tetrapod
: a four-footed animal; includes amphibians, reptiles, birds, and mammals

tunicate
: a sessile chordate that is a member of Urochordata

Urochordata
: the clade composed of the tunicates

vertebral column
: a series of separate bones that surround the spinal cord in vertebrates

water vascular system
: a system in echinoderms in which water is the circulatory fluid

Vertebrates

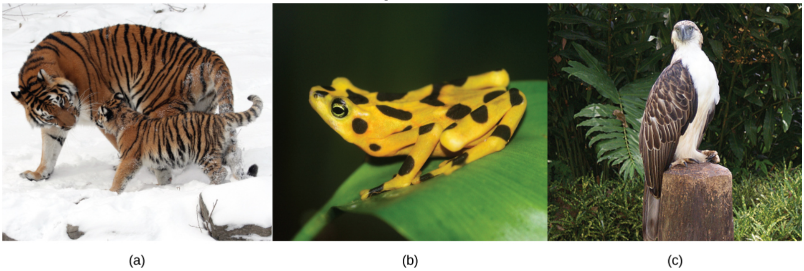
By the end of this section, you will be able to:

- Describe the difference between jawless and jawed fishes
- Explain the main characteristics of amphibians, reptiles, and birds
- Describe the derived characteristics in birds that facilitate flight
- Name and describe the distinguishing features of the three main groups of mammals
- Describe the derived features that distinguish primates from other animals

Vertebrates are among the most recognizable organisms of the animal kingdom ([link]). More than 62,000 vertebrate species have been identified. The vertebrate species now living represent only a small portion of the vertebrates that have existed. The best-known extinct vertebrates are the dinosaurs, a unique group of reptiles, reaching sizes not seen before or since in terrestrial animals. They were the dominant terrestrial animals for 150 million years, until they died out near the end of the Cretaceous period in a mass extinction. A great deal is known about the anatomy of the dinosaurs, given the preservation of their skeletal elements in the fossil record.

Examples of critically endangered vertebrate species include (a) the Siberian tiger *(Panthera tigris altaica*), (b) the Panamanian golden frog (*Atelopus zeteki*),

and (c) the Philippine eagle (*Pithecophaga jefferyi*). (credit a: modification of work by Dave Pape; credit b: modification of work by Brian Gratwicke; credit c: modification of work by "cuatrok77"/Flickr)



(a) Pacific hagfishes are scavengers that live on the ocean floor. (b) These parasitic sea lampreys attach to their lake trout host by suction and use their rough tongues to rasp away flesh in order to feed on the trout’s blood. (credit a: modification of work by Linda Snook, NOAA/CBNMS; credit b: modification of work by USGS) (a) This hammerhead shark is an example of a predatory cartilaginous fish. (b) This stingray blends into the sandy bottom of the ocean floor when it is feeding or awaiting prey. (credit a: modification of work by Masashi Sugawara; credit b: modification of work by "Sailn1"/Flickr) The (a) sockeye salmon and (b) coelacanth are both bony fishes of the Osteichthyes clade. The coelacanth, sometimes called a lobe-finned fish, was thought to have gone extinct in the Late Cretaceous period 100 million years ago until one was discovered in 1938 between Africa and Madagascar. (credit a: modification of work by Timothy Knepp, USFWS; credit b: modification of work by Robbie Cada)

Fishes

Modern fishes include an estimated 31,000 species. Fishes were the earliest vertebrates, and jawless fishes were the earliest of these. Jawless fishes—the present day hagfishes and lampreys—have a distinct cranium and complex sense organs including eyes, distinguishing them from the invertebrate chordates. The jawed fishes evolved later and are extraordinarily diverse today. Fishes are active feeders, rather than sessile, suspension feeders.

Jawless Fishes

Jawless fishes are **craniates** (which includes all the chordate groups except the tunicates and lancelets) that represent an ancient vertebrate lineage that arose over one half-billion years ago. Some of the earliest jawless fishes were the **ostracoderms** (which translates as "shell-skin"). Ostracoderms, now extinct, were vertebrate fishes encased in bony armor, unlike present-day jawless fishes, which lack bone in their scales.

The clade **Myxini** includes 67 species of hagfishes. **Hagfishes** are eel-like scavengers that live on the ocean floor and feed on dead invertebrates, other fishes, and marine mammals ([link]**a**). Hagfishes are entirely marine and are found in oceans around the world except for the polar regions. A unique feature of these animals is the slime glands beneath the skin

that are able to release an extraordinary amount of mucus through surface pores. This mucus may allow the hagfish to escape from the grip of predators. Hagfish are known to enter the bodies of dead or dying organisms to devour them from the inside.

(a) (b)

The skeleton of a hagfish is composed of cartilage, which includes a cartilaginous notochord, which runs the length of the body, and a skull. This notochord provides support to the fish's body. Although they are craniates, hagfishes are not vertebrates, since they do not replace the notochord with a vertebral column during development, as do the vertebrates.

The clade **Petromyzontidae** includes approximately 40 species of lampreys. **Lampreys** are similar to hagfishes in size and shape; however, lampreys have a brain case and incomplete vertebrae. Lampreys lack paired appendages and bone, as do the hagfishes. As adults, lampreys are characterized by a toothed, funnel-like sucking mouth. Some species are parasitic as adults, attaching to and feeding on the body fluids of fish ([link]**b**). Most species are free-living.

Lampreys live primarily in coastal and fresh waters and have a worldwide temperate region distribution. All species spawn in fresh waters. Eggs are fertilized externally, and the larvae are distinctly different from the adult form, spending 3 to 15 years as suspension feeders. Once they attain sexual maturity, the adults reproduce and die within days. Lampreys have a notochord as adults.

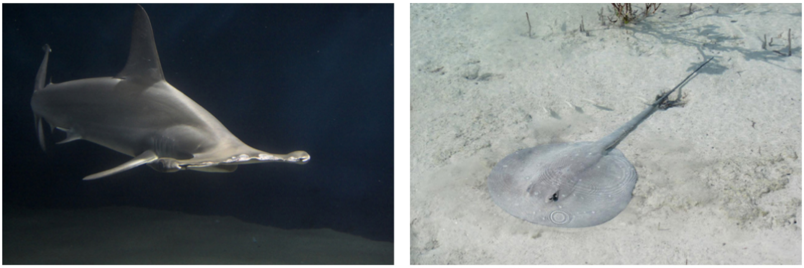
Jawed Fishes

Gnathostomes or "jaw-mouths" are vertebrates that have jaws and include both cartilaginous and bony fishes. One of the most significant developments in early vertebrate evolution was the origin of the jaw, which is a hinged structure attached to the cranium that allows an animal to grasp and tear its food. The evolution of jaws allowed early gnathostomes to exploit food resources that were unavailable to jawless fishes.

The clade **Chondrichthyes**, the cartilaginous fishes, is diverse, consisting of sharks ([link]**a**), rays, and skates, together with sawfishes and a few dozen species of fishes called *chimaeras*, or ghost sharks. Chondrichthyes have paired fins and a skeleton made of cartilage. This clade arose approximately 370 million years ago in the middle Devonian. They are thought to have descended from an extinct group that had a skeleton made of bone; thus, the cartilaginous skeleton of Chondrichthyes is a later

development. Parts of the shark skeleton are strengthened by granules of calcium carbonate, but this is not the same as bone.

Most cartilaginous fishes live in marine habitats, with a few species living in fresh water for some or all of their lives. Most sharks are carnivores that feed on live prey, either swallowing it whole or using their jaws and teeth to tear it into smaller pieces. Shark teeth likely evolved from the jagged scales that cover their skin. Some species of sharks and rays are suspension feeders that feed on plankton.



(a) (b)

Sharks have well-developed sense organs that aid them in locating prey, including a keen sense of smell and electroreception, the latter being perhaps the most sensitive of any animal. Organs called **ampullae of Lorenzini** allow sharks to detect the electromagnetic fields that are produced by all living things, including their prey. Electroreception has only been observed in aquatic or amphibious animals. Sharks, together with most fishes, also have a sense organ called the **lateral line**, which is used to detect movement and vibration in the

surrounding water, and a sense that is often considered homologous to “hearing” in terrestrial vertebrates. The lateral line is visible as a darker stripe that runs along the length of the fish’s body.

Sharks reproduce sexually and eggs are fertilized internally. Most species are ovoviviparous, that is, the fertilized egg is retained in the oviduct of the mother’s body, and the embryo is nourished by the egg yolk. The eggs hatch in the uterus and young are born alive and fully functional. Some species of sharks are oviparous: They lay eggs that hatch outside of the mother’s body. Embryos are protected by a shark egg case or “mermaid’s purse” that has the consistency of leather. The shark egg case has tentacles that snag in seaweed and give the newborn shark cover. A few species of sharks are viviparous, that is, the young develop within the mother’s body, and she gives live birth.

Rays and skates include more than 500 species and are closely related to sharks. They can be distinguished from sharks by their flattened bodies, pectoral fins that are enlarged and fused to the head, and gill slits on their ventral surface ([link]**b**). Like sharks, rays and skates have a cartilaginous skeleton. Most species are marine and live on the sea floor, with nearly a worldwide distribution.

Bony Fishes

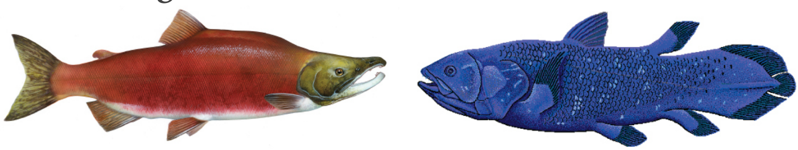
Members of the clade **Osteichthyes**, or bony fishes, are characterized by a bony skeleton. The vast majority of present-day fishes belong to this group, which consists of approximately 30,000 species, making it the largest class of vertebrates in existence today.

Nearly all bony fishes have an ossified skeleton with specialized bone cells (osteocytes) that produce and maintain a calcium phosphate matrix. This characteristic has only reverted in a few groups of Osteichthyes, such as sturgeons and paddlefish, which have primarily cartilaginous skeletons. The skin of bony fishes is often covered in overlapping scales, and glands in the skin secrete mucus that reduces drag when swimming and aids the fish in osmoregulation. Like sharks, bony fishes have a lateral line system that detects vibrations in water. Unlike sharks, some bony fish depend on their eyesight to locate prey. Bony fish are also unusual in possessing taste cells in the head and trunk region of the body that allow them to detect extremely small concentrations of molecules in the water.

All bony fishes, like the cartilaginous fishes, use gills to breathe. Water is drawn over gills that are located in chambers covered and ventilated by a protective, muscular flap called the operculum. Unlike sharks, bony fishes have a **swim bladder**, a gas-filled organ that helps to control the buoyancy of the fish. Bony fishes are further divided into two

clades with living members: **Actinopterygii** (ray-finned fishes) and **Sarcopterygii** (lobe-finned fishes).

The ray-finned fishes include many familiar fishes—tuna, bass, trout, and salmon ([link]**a**), among others. Ray-finned fishes are named for the form of their fins—webs of skin supported by bony spines called rays. In contrast, the fins of lobe-finned fishes are fleshy and supported by bone ([link]**b**). Living members of lobe-finned fishes include the less familiar lungfishes and coelacanth.



(a) (b)

(a) Most salamanders have legs and a tail, but respiration varies among species. (b) The Australian green tree frog is a nocturnal predator that lives in the canopies of trees near a water source. (credit a: modification of work by Valentina Storti; credit b: modification of work by Evan Pickett)A frog begins as a (a) tadpole and undergoes metamorphosis to become (b) a juvenile and finally (c) an adult. (credit: modification of work by Brian Gratwicke) Caecilians lack external limbs and are well adapted for a soil-burrowing lifestyle. (credit: modification of work by "cliff1066"/Flickr)

Amphibians

Amphibians are vertebrate tetrapods. **Amphibia** includes frogs, salamanders, and caecilians. The term amphibian means “dual life,” which is a reference to the metamorphosis that many frogs undergo from a tadpole to an adult and the mixture of aquatic and terrestrial environments in their life cycle. Amphibians evolved in the Devonian period and were the earliest terrestrial tetrapods.

As tetrapods, most amphibians are characterized by four well-developed limbs, although some species of salamanders and all caecilians possess only vestigial limbs. An important characteristic of extant amphibians is a moist, permeable skin, achieved by mucus glands. The moist skin allows oxygen and carbon dioxide exchange with the environment, a process called **cutaneous respiration**. All living adult amphibian species are carnivorous, and some terrestrial amphibians have a sticky tongue that is used to capture prey.

Amphibian Diversity

Amphibia comprise an estimated 6,500 extant species that inhabit tropical and temperate regions around the world. Amphibians can be divided into three clades: **Urodela** (“tailed-ones”), the salamanders and newts; **Anura** (“tail-less ones”), the frogs and toads; and **Apoda** (“legless ones”), the caecilians.

Living **salamanders** ([link]**a**) include approximately 500 species, some of which are aquatic, others terrestrial, and some that live on land only as adults. Adult salamanders usually have a generalized tetrapod body plan with four limbs and a tail. Some salamanders are lungless, and respiration occurs through the skin or external gills. Some terrestrial salamanders have primitive lungs; a few species have both gills and lungs.

(a)

(b)

Concept in Action

Watch this video about an unusually large salamander species.

Frogs ([link]**b**) are the most diverse group of amphibians, with approximately 5,000 species that live on all continents except Antarctica. Frogs have a body plan that is more specialized than the salamander body plan for movement on land. Adult frogs use their hind limbs to jump many times their body length on land. Frogs have a number of

modifications that allow them to avoid predators, including skin that acts as camouflage and defensive chemicals that are poisonous to predators secreted from glands in the skin.

Frog eggs are fertilized externally, as they are laid in moist environments. Frogs demonstrate a range of parental behaviors, with some species exhibiting little care, to species that carry eggs and tadpoles on their hind legs or backs. The life cycle consists of two stages: the larval stage followed by metamorphosis to an adult stage. The larval stage of a frog, the **tadpole**, is often a filter-feeding herbivore. Tadpoles usually have gills, a lateral line system, long-finned tails, but no limbs. At the end of the tadpole stage, frogs undergo a gradual metamorphosis into the adult form. During this stage, the gills and lateral line system disappear, and four limbs develop. The jaws become larger and are suited for carnivorous feeding, and the digestive system transforms into the typical short gut of a predator. An eardrum and air-breathing lungs also develop. These changes during metamorphosis allow the larvae to move onto land in the adult stage ([link]).

Caecilians comprise an estimated 185 species. They

lack external limbs and resemble giant earthworms. They inhabit soil and are found primarily in the tropics of South America, Africa, and southern Asia where they are adapted for a soil-burrowing lifestyle and are nearly blind. Unlike most of the other amphibians that breed in or near water, reproduction in a drier soil habitat means that caecilians must utilize internal fertilization, and most species give birth to live young ([link]).

(a) Crocodilians, such as this Siamese crocodile, provide parental care for their offspring. (b) This Jackson's chameleon blends in with its surroundings. (c) The garter snake belongs to the genus *Thamnophis*, the most widely distributed reptile genus in North America. (d) The African spurred tortoise lives at the southern edge of the Sahara Desert. It is the third largest tortoise in the world. (credit a: modification of work by Keshav Mukund Kandhadai; credit c: modification of work by Steve Jurvetson; credit d: modification of work by Jim Bowen) (a) Primary feathers are located at the wing tip and provide thrust; secondary feathers are located close to the body and provide lift. (b)

Many birds have hollow pneumatic bones, which make flight easier.

Reptiles and Birds

The **amniotes**—reptiles, birds, and mammals—are distinguished from amphibians by their terrestrially adapted (shelled) egg and an embryo protected by amniotic membranes. The evolution of amniotic membranes meant that the embryos of amniotes could develop within an aquatic environment inside the egg. This led to less dependence on a water environment for development and allowed the amniotes to invade drier areas. This was a significant evolutionary change that distinguished them from amphibians, which were restricted to moist environments due to their shell-less eggs. Although the shells of various amniotic species vary significantly, they all allow retention of water. The membranes of the amniotic egg also allowed gas exchange and sequestering of wastes within the enclosure of an eggshell. The shells of bird eggs are composed of calcium carbonate and are hard and brittle, but possess pores for gas and water exchange. The shells of reptile eggs are more leathery and pliable. Most mammals do not lay eggs; however, even with internal gestation, amniotic membranes are still present.

In the past, the most common division of amniotes has been into classes Mammalia, Reptilia, and Aves.

Birds are descended, however, from dinosaurs, so this classical scheme results in groups that are not true clades. We will discuss birds as a group distinct from reptiles with the understanding that this does not reflect evolutionary history.

Reptiles

Reptiles are tetrapods. Limbless reptiles—snakes—may have vestigial limbs and, like caecilians, are classified as tetrapods because they are descended from four-limbed ancestors. Reptiles lay shelled eggs on land. Even aquatic reptiles, like sea turtles, return to the land to lay eggs. They usually reproduce sexually with internal fertilization. Some species display ovoviviparity, with the eggs remaining in the mother's body until they are ready to hatch. Other species are viviparous, with the offspring born alive.

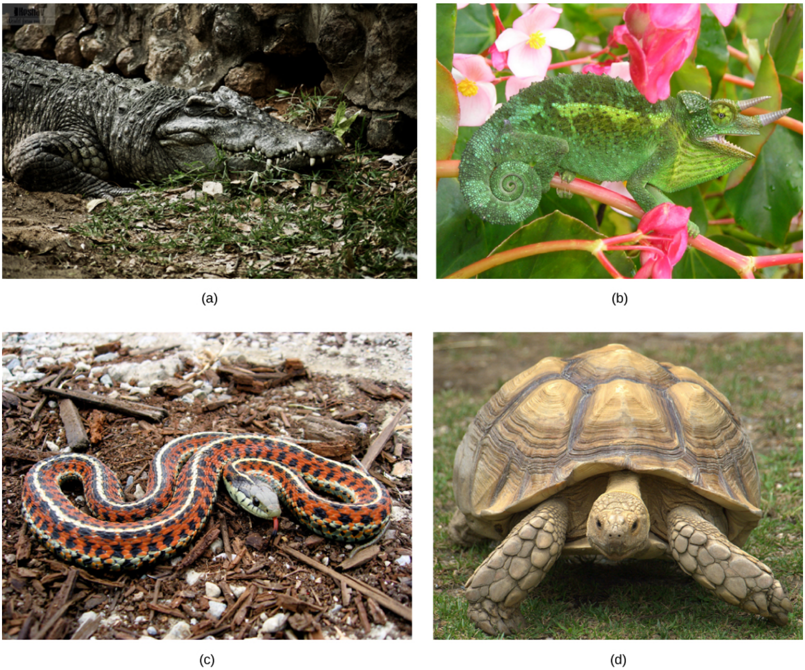
One of the key adaptations that permitted reptiles to live on land was the development of their scaly skin, containing the protein keratin and waxy lipids, which prevented water loss from the skin. This occlusive skin means that reptiles cannot use their skin for respiration, like amphibians, and thus all must breathe with lungs. In addition, reptiles conserve valuable body water by excreting nitrogen in the form of uric acid paste. These characteristics, along with the shelled, amniotic egg, were the major reasons why reptiles became so successful in

colonizing a variety of terrestrial habitats far from water.

Reptiles are ectotherms, that is, animals whose main source of body heat comes from the environment. Behavioral maneuvers, like basking to heat themselves, or seeking shade or burrows to cool off, help them regulate their body temperature,

Class Reptilia includes diverse species classified into four living clades. These are the Crocodilia, Sphenodontia, Squamata, and Testudines.

The **Crocodilia** (“small lizard”) arose approximately 84 million years ago, and living species include alligators, crocodiles, and caimans. Crocodilians ([link]**a**) live throughout the tropics of Africa, South America, the southeastern United States, Asia, and Australia. They are found in freshwater habitats, such as rivers and lakes, and spend most of their time in water. Some species are able to move on land due to their semi-erect posture.



The **Sphenodontia** (“wedge tooth”) arose in the Mesozoic Era and includes only one living genus, *Tuatara*, with two species that are found in New Zealand. There are many fossil species extending back to the Triassic period (250–200 million years ago). Although the tuataras resemble lizards, they are anatomically distinct and share characteristics that are found in birds and turtles.

Squamata (“scaly”) arose in the late Permian; living species include lizards and snakes, which are the largest extant clade of reptiles ([link]**b**). Lizards differ from snakes by having four limbs, eyelids, and external ears, which are lacking in snakes. Lizard species range in size from chameleons and geckos

that are a few centimeters in length to the Komodo dragon, which is about 3 meters in length.

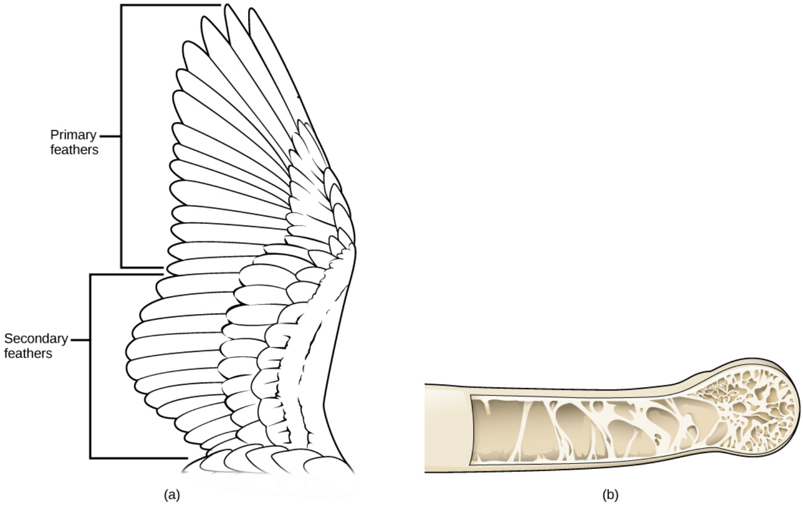
Snakes are thought to have descended from either burrowing lizards or aquatic lizards over 100 million years ago ([link]**c**). Snakes comprise about 3,000 species and are found on every continent except Antarctica. They range in size from 10 centimeter-long thread snakes to 7.5 meter-long pythons and anacondas. All snakes are carnivorous and eat small animals, birds, eggs, fish, and insects.

Turtles are members of the clade **Testudines** ("having a shell") ([link]**d**). Turtles are characterized by a bony or cartilaginous shell, made up of the carapace on the back and the plastron on the ventral surface, which develops from the ribs. Turtles arose approximately 200 million years ago, predating crocodiles, lizards, and snakes. Turtles lay eggs on land, although many species live in or near water. Turtles range in size from the speckled padloper tortoise at 8 centimeters (3.1 inches) to the leatherback sea turtle at 200 centimeters (over 6 feet). The term "turtle" is sometimes used to describe only those species of Testudines that live in the sea, with the terms "tortoise" and "terrapin" used to refer to species that live on land and in fresh water, respectively.

Birds

Data now suggest that birds belong within the reptile clade, but they display a number of unique adaptations that set them apart. Unlike the reptiles, birds are endothermic, meaning they generate their own body heat through metabolic processes. The most distinctive characteristic of birds is their feathers, which are modified reptilian scales. Birds have several different types of feathers that are specialized for specific functions, like contour feathers that streamline the bird's exterior and loosely structured **down feathers** that insulate ([link]**a**).

Feathers not only permitted the earliest birds to glide, and ultimately engage in flapping flight, but they insulated the bird's body, assisting the maintenance of endothermy, even in cooler temperatures. Powering a flying animal requires economizing on the amount of weight carried. As body weight increases, the muscle output and energetic cost required for flying increase. Birds have made several modifications to reduce body weight, including hollow or **pneumatic bones** ([link]**b**) with air spaces that may be connected to air sacs and cross-linked struts within their bones to provide structural reinforcement. Parts of the vertebral skeleton and braincase are fused to increase its strength while lightening its weight. Most species of bird only possess one ovary rather than two, and no living birds have teeth in their jaw, further reducing body mass.



Birds possess a system of air sacs branching from their primary airway that divert the path of air so that it passes unidirectionally through the lung, during both inspiration and expiration. Unlike mammalian lungs in which air flows in two directions as it is breathed in and out, air flows continuously through the bird’s lung to provide a more efficient system of gas exchange.

The platypus (left), a monotreme, possesses a leathery beak and lays eggs rather than giving birth to live young. An echidna, another monotreme, is shown in the right photo. (credit “echidna”: modification of work by Barry Thomas) The Tasmanian devil is one of several marsupials native to Australia. (credit: Wayne McLean)Primates can be divided into prosimians, such as the (a) lemur, and anthropoids. Anthropoids include monkeys, such as the (b) howler monkey; lesser apes, such as the (c) gibbon; and great apes, such as the (d) chimpanzee,

(e) bonobo, (f) gorilla, and (g) orangutan. (credit a: modification of work by Frank Vassen; credit b: modification of work by Xavi Talleda; credit d: modification of work by Aaron Logan; credit e: modification of work by Trisha Shears; credit f: modification of work by Dave Proffer; credit g: modification of work by Julie Langford)

Mammals

Mammals are vertebrates that have hair and mammary glands used to provide nutrition for their young. Certain features of the jaw, skeleton, skin, and internal anatomy are also unique to mammals. The presence of hair is one of the key characteristics of a mammal. Although it is not very extensive in some groups, such as whales, hair has many important functions for mammals. Mammals are endothermic, and hair provides insulation by trapping a layer of air close to the body to retain metabolic heat. Hair also serves as a sensory mechanism through specialized hairs called vibrissae, better known as whiskers. These attach to nerves that transmit touch information, which is particularly useful to nocturnal or burrowing mammals. Hair can also provide protective coloration.

Mammalian skin includes secretory glands with various functions. **Sebaceous glands** produce a lipid mixture called sebum that is secreted onto the

hair and skin for water resistance and lubrication. Sebaceous glands are located over most of the body. **Sudoriferous glands** produce sweat and scent, which function in thermoregulation and communication, respectively. **Mammary glands** produce milk that is used to feed newborns. While male monotremes and eutherians possess mammary glands, male marsupials do not.

The skeletal system of mammals possesses unique features that differentiate them from other vertebrates. Most mammals have **heterodont teeth**, meaning they have different types and shapes of teeth that allow them to feed on different kinds of foods. These different types of teeth include the incisors, the canines, premolars, and molars. The first two types are for cutting and tearing, whereas the latter two types are for crushing and grinding. Different groups have different proportions of each type, depending on their diet. Most mammals are also **diphyodonts**, meaning they have two sets of teeth in their lifetime: deciduous or “baby” teeth, and permanent teeth. In other vertebrates, the teeth can be replaced throughout life.

Modern mammals are divided into three broad groups: monotremes, marsupials, and eutherians (or placental mammals). The eutherians, or placental mammals, and the marsupials collectively are called therian mammals, whereas monotremes are called metatherians.

There are three living species of **monotremes**: the platypus and two species of echidnas, or spiny anteaters ([link]). The platypus and one species of echidna are found in Australia, whereas the other species of echidna is found in New Guinea. Monotremes are unique among mammals, as they lay leathery eggs, similar to those of reptiles, rather than giving birth to live young. However, the eggs are retained within the mother’s reproductive tract until they are almost ready to hatch. Once the young hatch, the female begins to secrete milk from pores in a ridge of mammary tissue along the ventral side of her body. Like other mammals, monotremes are endothermic but regulate body temperatures somewhat lower (90 °F, 32 °C) than placental mammals do (98 °F, 37 °C). Like reptiles, monotremes have one posterior opening for urinary, fecal, and reproductive products, rather than three separate openings like placental mammals do. Adult monotremes lack teeth.

Marsupials are found primarily in Australia and nearby islands, although about 100 species of opossums and a few species of two other families are found in the Americas. Australian marsupials

number over 230 species and include the kangaroo, koala, bandicoot, and Tasmanian devil ([link]). Most species of marsupials possess a pouch in which the young reside after birth, receiving milk and continuing to develop. Before birth, marsupials have a less complex placental connection, and the young are born much less developed than in placental mammals.

Eutherians are the most widespread of the mammals, occurring throughout the world. There are several groups of eutherians, including Insectivora, the insect eaters; Edentata, the toothless anteaters; Rodentia, the rodents; Chiroptera, the bats; Cetacea, the aquatic mammals including whales; Carnivora, carnivorous mammals including dogs, cats, and bears; and Primates, which includes humans. **Eutherian mammals** are sometimes called placental mammals, because all species have a complex placenta that connects a fetus to the

mother, allowing for gas, fluid, waste, and nutrient exchange. While other mammals may possess a less complex placenta or briefly have a placenta, all eutherians have a complex placenta during gestation.

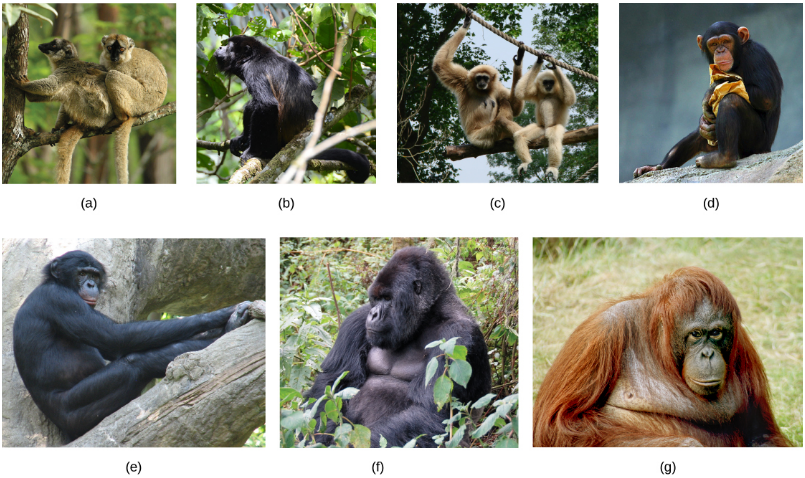
Primates

Order **Primates** of class Mammalia includes lemurs, tarsiers, monkeys, and the apes, which include humans. Non-human primates live primarily in tropical or subtropical regions of South America, Africa, and Asia. They range in size from the mouse lemur at 30 grams (1 ounce) to the mountain gorilla at 200 kilograms (441 pounds). The characteristics and evolution of primates are of particular interest to us as they allow us to understand the evolution of our own species.

All primate species have adaptations for climbing trees, as they all descended from tree-dwellers, although not all species are arboreal. This arboreal heritage of primates resulted in hands and feet that are adapted for **brachiation**, or climbing and swinging through trees. These adaptations include, but are not limited to 1) a rotating shoulder joint, 2) a big toe that is widely separated from the other toes and thumbs that are widely separated from fingers (except humans), which allow for gripping branches, and 3) **stereoscopic vision**, two overlapping visual fields, which allows for the depth

perception necessary to gauge distance. Other characteristics of primates are brains that are larger than those of many other mammals, claws that have been modified into flattened nails, typically only one offspring per pregnancy, and a trend toward holding the body upright.

Order Primates is divided into two groups: prosimians and anthropoids. **Prosimians** include the bush babies of Africa, the lemurs of Madagascar, and the lorises, pottos, and tarsiers of Southeast Asia. **Anthropoids** include monkeys, lesser apes, and great apes ([link]). In general, prosimians tend to be nocturnal, smaller in size than anthropoids, and have relatively smaller brains compared to anthropoids.



Section Summary

The earliest vertebrates that diverged from the invertebrate chordates were the jawless fishes. Hagfishes are eel-like scavengers that feed on dead invertebrates and other fishes. Lampreys are characterized by a toothed, funnel-like sucking mouth, and some species are parasitic on other fishes. Gnathostomes include the jawed fishes (cartilaginous and bony fishes) as well as all other tetrapods. Cartilaginous fishes include sharks, rays, skates, and ghost sharks. Bony fishes can be further divided into ray-finned and lobe-finned fishes.

As tetrapods, most amphibians are characterized by four well-developed limbs, although some species of salamanders and all caecilians are limbless. Amphibians have a moist, permeable skin used for cutaneous respiration. Amphibia can be divided into three clades: salamanders (Urodela), frogs (Anura), and caecilians (Apoda). The life cycle of amphibians consists of two distinct stages: the larval stage and metamorphosis to an adult stage.

The amniotes are distinguished from amphibians by the presence of a terrestrially adapted egg protected by amniotic membranes. The amniotes include reptiles, birds, and mammals. A key adaptation that permitted reptiles to live on land was the development of scaly skin. Reptilia includes four living clades: Crocodilia (crocodiles and alligators), Sphenodontia (tuataras), Squamata (lizards and snakes), and Testudines (turtles).

Birds are endothermic amniotes. Feathers act as insulation and allow for flight. Birds have pneumatic bones that are hollow rather than tissue-filled. Airflow through bird lungs travels in one direction. Birds evolved from dinosaurs.

Mammals have hair and mammary glands. Mammalian skin includes various secretory glands. Mammals are endothermic, like birds. There are three groups of mammals living today: monotremes, marsupials, and eutherians. Monotremes are unique among mammals as they lay eggs, rather than giving birth to live young. Eutherian mammals have a complex placenta.

There are 16 extant (living) orders of eutherian mammals. Humans are most closely related to Primates, all of which have adaptations for climbing trees, although not all species are arboreal. Other characteristics of primates are brains that are larger than those of other mammals, claws that have been modified into flattened nails, and typically one young per pregnancy, stereoscopic vision, and a trend toward holding the body upright. Primates are divided into two groups: prosimians and anthropoids.

Review Questions

Members of Chondrichthyes differ from members of Osteichthyes by having a ______.

1. jaw
2. bony skeleton
3. cartilaginous skeleton
4. two sets of paired fins

C

Squamata includes ____.

1. crocodiles and alligators
2. turtles
3. tuataras
4. lizards and snakes

D

Sudoriferous glands produce ______.

1. sweat
2. lipids
3. sebum
4. milk

A

Which of the following is a Monotreme?

1. kangaroo
2. koala
3. bandicoot
4. platypus

D

Free Response

What can be inferred about the evolution of the cranium and the vertebral column from examining hagfishes and lampreys?

Comparison of hagfishes with lampreys shows that the cranium evolved first in early vertebrates, as it is seen in hagfishes, which evolved earlier than lampreys. This was followed by evolution of the vertebral column, a primitive form of which is seen in lampreys and not in hagfishes.

Explain why frogs are restricted to a moist environment.

A moist environment is required as frog eggs lack a shell and dehydrate quickly in dry environments.

Describe three adaptations that allow for flight in birds.

Birds have feathers that streamline the bird body and assist in flight. They also have pneumatic bones that are hollow rather than tissue-filled. Birds are endothermic, which allows for a higher metabolism demanded by flight.

Glossary

Actinopterygii
: ray-finned fishes

amniote
: a clade of animals that possesses an amniotic egg; includes reptiles (including birds) and mammals

Amphibia
: frogs, salamanders, and caecilians

ampulla of Lorenzini
: a sensory organ that allows sharks to detect

electromagnetic fields produced by living things

anthropoids
: a clade consisting of monkeys, apes, and humans

Anura
: frogs

Apoda
: caecilians

brachiation
: swinging through trees

caecilian
: a legless amphibian that belongs to clade Apoda

Chondrichthyes
: jawed fishes with paired fins and a skeleton made of cartilage

craniate
: a proposed clade of chordates that includes all groups except the tunicates and lancelets

Crocodilia
: crocodiles and alligators

cutaneous respiration
: gas exchange through the skin

diphyodont
refers to the possession of two sets of teeth in a lifetime

down feather
feather specialized for insulation

eutherian mammal
a mammal with a complex placenta, which connects a fetus to the mother; sometimes called placental mammals

frog
a tail-less amphibian that belongs to clade Anura

gnathostome
a jawed fish

hagfish
an eel-like jawless fish that lives on the ocean floor and is a scavenger

heterodont teeth
different types of teeth modified by different purposes

lamprey
a jawless fish characterized by a toothed, funnel-like, sucking mouth

lateral line
the sense organ that runs the length of a fish's

body, used to detect vibration in the water

mammal
: one of the groups of endothermic vertebrates that possess hair and mammary glands

mammary gland
: in female mammals, a gland that produces milk for newborns

marsupial
: one of the groups of mammals that includes the kangaroo, koala, bandicoot, Tasmanian devil, and several other species; young develop within a pouch

monotreme
: an egg-laying mammal

Myxini
: hagfishes

Osteichthyes
: bony fishes

ostracoderm
: one of the earliest jawless fishes covered in bone

Petromyzontidae
: the clade of lampreys

pneumatic bone

an air-filled bone

Primates
: includes lemurs, tarsiers, monkeys, apes, and humans

prosimians
: a group of primates that includes bush babies of Africa, lemurs of Madagascar, and lorises, pottos, and tarsiers of southeast Asia

salamander
: a tailed amphibian that belongs to the clade Urodela

Sarcopterygii
: lobe-finned fishes

sebaceous gland
: in mammals, a skin gland that produce a lipid mixture called sebum

Sphenodontia
: the reptilian clade that includes the tuataras

Squamata
: the reptilian clade of lizards and snakes

stereoscopic vision
: two overlapping fields of vision from the eyes that produces depth perception

sudoriferous gland

a gland in mammals that produces sweat and scent molecules

swim bladder
: in fishes, a gas filled organ that helps to control the buoyancy of the fish

tadpole
: the larval stage of a frog

Testudines
: turtles

Urodela
: salamanders

Population Demographics and Dynamics

By the end of this section, you will be able to:

- Describe how ecologists measure population size and density
- Describe three different patterns of population distribution
- Use life tables to calculate mortality rates
- Describe the three types of survivorship curves and relate them to specific populations

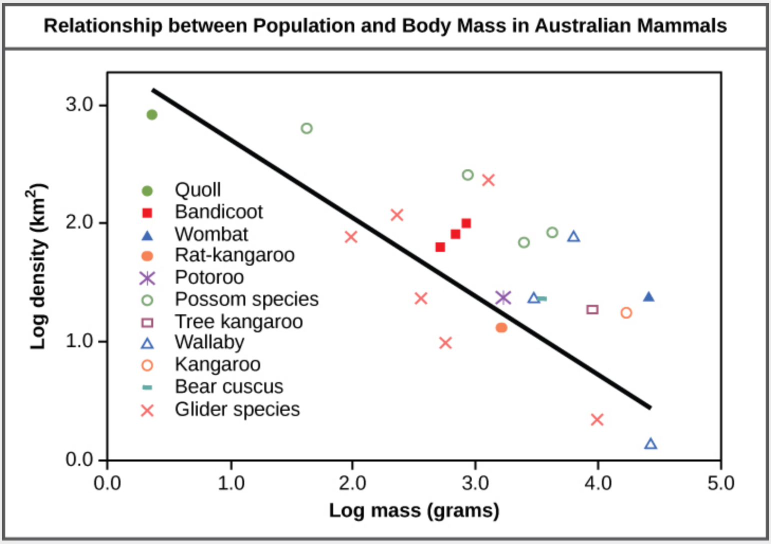
Populations are dynamic entities. Their size and composition fluctuate in response to numerous factors, including seasonal and yearly changes in the environment, natural disasters such as forest fires and volcanic eruptions, and competition for resources between and within species. The statistical study of populations is called **demography**: a set of mathematical tools designed to describe populations and investigate how they change. Many of these tools were actually designed to study human populations. For example, **life tables**, which detail the life expectancy of individuals within a population, were initially developed by life insurance companies to set insurance rates. In fact, while the term “demographics” is sometimes assumed to mean a study of human populations, all living populations can be studied using this approach.

Population Size and Density

Populations are characterized by their **population size** (total number of individuals) and their **population density** (number of individuals per unit area). A population may have a large number of individuals that are distributed densely, or sparsely. There are also populations with small numbers of individuals that may be dense or very sparsely distributed in a local area. Population size can affect potential for adaptation because it affects the amount of genetic variation present in the population. Density can have effects on interactions within a population such as competition for food and the ability of individuals to find a mate. Smaller organisms tend to be more densely distributed than larger organisms ([link]).

Visual Connection

Australian mammals show a typical inverse relationship between population density and body size.



As this graph shows, population density typically decreases with increasing body size. Why do you think this is the case?

Estimating Population Size

The most accurate way to determine population size is to count all of the individuals within the area. However, this method is usually not logistically or economically feasible, especially when studying large areas. Thus, scientists usually study populations by sampling a representative portion of each habitat and use this sample to make inferences about the population as a whole. The methods used to sample populations to determine their size and density are typically tailored to the characteristics of the organism being studied. For immobile organisms

such as plants, or for very small and slow-moving organisms, a quadrat may be used. A **quadrat** is a wood, plastic, or metal square that is randomly located on the ground and used to count the number of individuals that lie within its boundaries. To obtain an accurate count using this method, the square must be placed at random locations within the habitat enough times to produce an accurate estimate. This counting method will provide an estimate of both population size and density. The number and size of quadrat samples depends on the type of organisms and the nature of their distribution.

For smaller mobile organisms, such as mammals, a technique called **mark and recapture** is often used. This method involves marking a sample of captured animals in some way and releasing them back into the environment to mix with the rest of the population; then, a new sample is captured and scientists determine how many of the marked animals are in the new sample. This method assumes that the larger the population, the lower the percentage of marked organisms that will be recaptured since they will have mixed with more unmarked individuals. For example, if 80 field mice are captured, marked, and released into the forest, then a second trapping 100 field mice are captured and 20 of them are marked, the population size (N) can be determined using the following equation:

number marked first catch $\times$ total number second catch

$$\text{number marked second catch} = N$$

Using our example, the population size would be 400.

$$80 \times 100\ 20 = 400$$

These results give us an estimate of 400 total individuals in the original population. The true number usually will be a bit different from this because of chance errors and possible bias caused by the sampling methods.
Species may have a random, clumped, or uniform distribution. Plants such as (a) dandelions with wind-dispersed seeds tend to be randomly distributed. Animals such as (b) elephants that travel in groups exhibit a clumped distribution. Territorial birds such as (c) penguins tend to have a uniform distribution. (credit a: modification of work by Rosendahl; credit b: modification of work by Rebecca Wood; credit c: modification of work by Ben Tubby)

Species Distribution

In addition to measuring density, further information about a population can be obtained by looking at the distribution of the individuals throughout their range. A **species distribution pattern** is the distribution of individuals within a habitat at a particular point in time—broad categories of patterns are used to describe them.

Individuals within a population can be distributed at random, in groups, or equally spaced apart (more or less). These are known as random, clumped, and uniform distribution patterns, respectively ([link]). Different distributions reflect important aspects of the biology of the species; they also affect the mathematical methods required to estimate population sizes. An example of random distribution occurs with dandelion and other plants that have wind-dispersed seeds that germinate wherever they happen to fall in favorable environments. A clumped distribution, may be seen in plants that drop their seeds straight to the ground, such as oak trees; it can also be seen in animals that live in social groups (schools of fish or herds of elephants). Uniform distribution is observed in plants that secrete substances inhibiting the growth of nearby individuals (such as the release of toxic chemicals by sage plants). It is also seen in territorial animal species, such as penguins that maintain a defined territory for nesting. The territorial defensive behaviors of each individual create a regular pattern of distribution of similar-sized territories and individuals within those territories. Thus, the distribution of the individuals within a population provides more information about how they interact with each other than does a simple density measurement. Just as lower density species might have more difficulty finding a mate, solitary species with a random distribution might have a similar difficulty when compared to social species clumped

together in groups.

(a) (b) (c)

Survivorship curves show the distribution of individuals in a population according to age. Humans and most mammals have a Type I survivorship curve, because death primarily occurs in the older years. Birds have a Type II survivorship curve, as death at any age is equally probable. Trees have a Type III survivorship curve because very few survive the younger years, but after a certain age, individuals are much more likely to survive.

Demography

While population size and density describe a population at one particular point in time, scientists must use demography to study the dynamics of a population. Demography is the statistical study of population changes over time: birth rates, death rates, and life expectancies. These population characteristics are often displayed in a life table.

Life Tables

Life tables provide important information about the life history of an organism and the life expectancy of individuals at each age. They are modeled after actuarial tables used by the insurance industry for estimating human life expectancy. Life tables may include the probability of each age group dying before their next birthday, the percentage of surviving individuals dying at a particular age interval (their **mortality rate**, and their life expectancy at each interval. An example of a life table is shown in [link] from a study of Dall mountain sheep, a species native to northwestern North America. Notice that the population is divided into age intervals (column A). The mortality rate (per 1000) shown in column D is based on the number of individuals dying during the age interval (column B), divided by the number of individuals surviving at the beginning of the interval (Column C) multiplied by 1000.

$$\text{mortality rate} = \frac{\text{number of individuals dying}}{\text{number of individuals surviving}} \times 1000$$

For example, between ages three and four, 12 individuals die out of the 776 that were remaining from the original 1000 sheep. This number is then multiplied by 1000 to give the mortality rate per thousand.

$$\text{mortality rate} = \frac{12}{776} \times 1000 \approx 15.5$$

As can be seen from the mortality rate data (column D), a high death rate occurred when the sheep were

between six months and a year old, and then increased even more from 8 to 12 years old, after which there were few survivors. The data indicate that if a sheep in this population were to survive to age one, it could be expected to live another 7.7 years on average, as shown by the life-expectancy numbers in column E.

Life Table of Dall Mountain Sheep [footnote] Data Adapted from Edward S. Deevey, Jr., "Life Tables for Natural Populations of Animals," *The Quarterly Review of*

Biology 22, no. 4 (December 1947): 283–314.

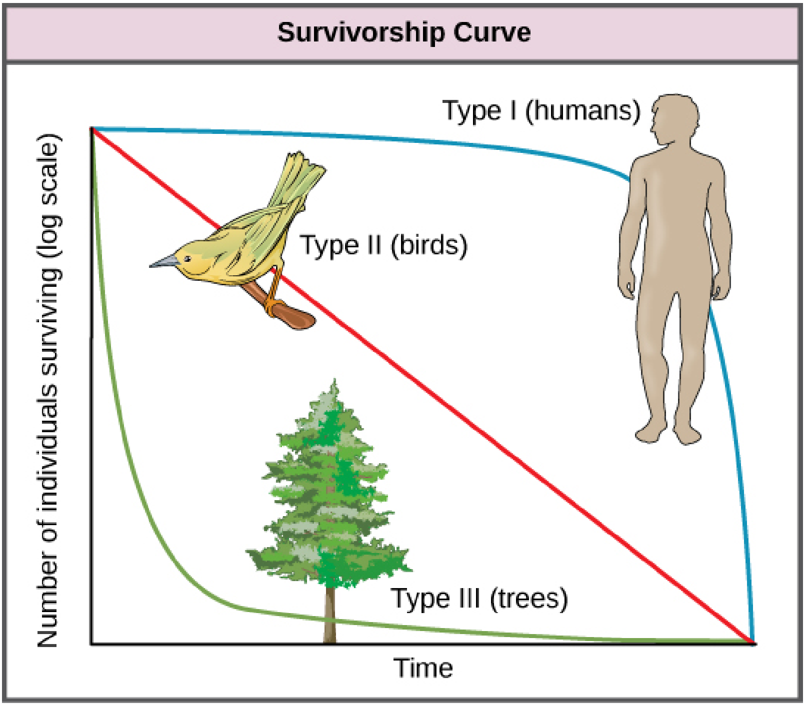
A Age interval (years)	B Number dying in age interval out of 1000 born	C Number surviving at beginning of age interval out of 1000 born	D Mortality rate per 1000 alive at beginning of age interval	E Life expectancy or mean lifetime remaining to those attaining age interval
0–0.5	54	1000	54.0	7.06
0.5–1	145	946	153.3	
1–2	12	801	15.0	7.7
2–3	13	789	16.5	6.8
3–4	12	776	15.5	5.9
4–5	30	764	39.3	5.0
5–6	46	734	62.7	4.2
6–7	48	688	69.8	3.4
7–8	69	640	107.8	2.6
8–9	132	571	231.2	1.9
9–10	187	439	426.0	1.3
10–11	156	252	619.0	0.9
11–12	90	96	937.5	0.6
12–13	3	6	500.0	1.2
13–14	3	3	1000	0.7

This life table of *Ovis dalli* shows the number of deaths, number of survivors, mortality rate, and life expectancy at each age interval for Dall mountain sheep.

Survivorship Curves

Another tool used by population ecologists is a **survivorship curve**, which is a graph of the number of individuals surviving at each age interval versus time. These curves allow us to compare the life histories of different populations ([link]). There are three types of survivorship curves. In a type I curve, mortality is low in the early and middle years and occurs mostly in older individuals. Organisms exhibiting a type I survivorship typically produce few offspring and provide good care to the offspring increasing the likelihood of their survival. Humans and most mammals exhibit a type I survivorship curve. In type II curves, mortality is relatively constant throughout the entire life span, and mortality is equally likely to occur at any point in the life span. Many bird populations provide examples of an intermediate or type II survivorship curve. In type III survivorship curves, early ages experience the highest mortality with much lower mortality rates for organisms that make it to advanced years. Type III organisms typically produce large numbers of offspring, but provide very little or no care for them. Trees and marine invertebrates exhibit a type III survivorship curve

because very few of these organisms survive their younger years, but those that do make it to an old age are more likely to survive for a relatively long period of time.



Section Summary

Populations are individuals of a species that live in a particular habitat. Ecologists measure characteristics of populations: size, density, and distribution pattern. Life tables are useful to calculate life expectancies of individual population members. Survivorship curves show the number of individuals surviving at each age interval plotted versus time.

[link] As this graph shows, population density typically decreases with increasing body size. Why do you think this is the case?

[link] Smaller animals require less food and others resources, so the environment can support more of them per unit area.

Multiple Choice

Which of the following methods will provide information to an ecologist about both the size and density of a population?

1. mark and recapture
2. mark and release
3. quadrat
4. life table

C

Which of the following is best at showing the life expectancy of an individual within a

population?

1. quadrat
2. mark and recapture
3. survivorship curve
4. life table

D

Human populations have which type of survivorship curve?

1. Type I
2. Type II
3. Type III
4. Type IV

A

Free Response

Describe how a researcher would determine the size of a penguin population in Antarctica using the mark and release method.

The researcher would mark a certain number of penguins with a tag, release them back into the population, and, at a later time, recapture penguins to see what percentage was tagged. This percentage would allow an estimation of the size of the penguin population.

Glossary

demography
: the statistical study of changes in populations over time

life table
: a table showing the life expectancy of a population member based on its age

mark and recapture
: a method used to determine population size in mobile organisms

mortality rate
: the proportion of population surviving to the beginning of an age interval that dies during that age interval

population density
: the number of population members divided by the area being measured

population size

the number of individuals in a population

quadrat
: a square within which a count of individuals is made that is combined with other such counts to determine population size and density in slow moving or stationary organisms

species distribution pattern
: the distribution of individuals within a habitat at a given point in time

survivorship curve
: a graph of the number of surviving population members versus the relative age of the member

Population Growth and Regulation
By the end of this section, you will be able to:

- Explain the characteristics of and differences between exponential and logistic growth patterns
- Give examples of exponential and logistic growth in natural populations
- Give examples of how the carrying capacity of a habitat may change
- Compare and contrast density-dependent growth regulation and density-independent growth regulation giving examples

Population ecologists make use of a variety of methods to model population dynamics. An accurate model should be able to describe the changes occurring in a population and predict future changes.

Population Growth

The two simplest models of population growth use deterministic equations (equations that do not account for random events) to describe the rate of change in the size of a population over time. The first of these models, exponential growth, describes theoretical populations that increase in numbers without any limits to their growth. The second

model, logistic growth, introduces limits to reproductive growth that become more intense as the population size increases. Neither model adequately describes natural populations, but they provide points of comparison.

Exponential Growth

Charles Darwin, in developing his theory of natural selection, was influenced by the English clergyman Thomas Malthus. Malthus published his book in 1798 stating that populations with abundant natural resources grow very rapidly; however, they limit further growth by depleting their resources. The early pattern of accelerating population size is called **exponential growth**.

The best example of exponential growth in organisms is seen in bacteria. Bacteria are prokaryotes that reproduce largely by binary fission. This division takes about an hour for many bacterial species. If 1000 bacteria are placed in a large flask with an abundant supply of nutrients (so the nutrients will not become quickly depleted), the number of bacteria will have doubled from 1000 to 2000 after just an hour. In another hour, each of the 2000 bacteria will divide, producing 4000 bacteria. After the third hour, there should be 8000 bacteria in the flask. The important concept of exponential growth is that the growth rate—the number of organisms added in each reproductive generation—

is itself increasing; that is, the population size is increasing at a greater and greater rate. After 24 of these cycles, the population would have increased from 1000 to more than 16 billion bacteria. When the population size, *N*, is plotted over time, a **J-shaped growth curve** is produced ([link]**a**).

The bacteria-in-a-flask example is not truly representative of the real world where resources are usually limited. However, when a species is introduced into a new habitat that it finds suitable, it may show exponential growth for a while. In the case of the bacteria in the flask, some bacteria will die during the experiment and thus not reproduce; therefore, the growth rate is lowered from a maximal rate in which there is no mortality. The growth rate of a population is largely determined by subtracting the **death rate**, *D*, (number organisms that die during an interval) from the **birth rate**, *B*, (number organisms that are born during an interval). The growth rate can be expressed in a simple equation that combines the birth and death rates into a single factor: *r*. This is shown in the following formula:

$$\text{Population growth} = \text{rN}$$

The value of *r* can be positive, meaning the population is increasing in size (the rate of change is positive); or negative, meaning the population is decreasing in size; or zero, in which case the population size is unchanging, a condition known as

zero population growth.

When resources are unlimited, populations exhibit (a) exponential growth, shown in a J-shaped curve. When resources are limited, populations exhibit (b) logistic growth. In logistic growth, population expansion decreases as resources become scarce, and it levels off when the carrying capacity of the environment is reached. The logistic growth curve is S-shaped.

Logistic Growth

Extended exponential growth is possible only when infinite natural resources are available; this is not the case in the real world. Charles Darwin recognized this fact in his description of the "struggle for existence," which states that individuals will compete (with members of their own or other species) for limited resources. The successful ones are more likely to survive and pass on the traits that made them successful to the next generation at a greater rate (natural selection). To model the reality of limited resources, population ecologists developed the **logistic growth** model.

Carrying Capacity and the Logistic Model

In the real world, with its limited resources, exponential growth cannot continue indefinitely. Exponential growth may occur in environments

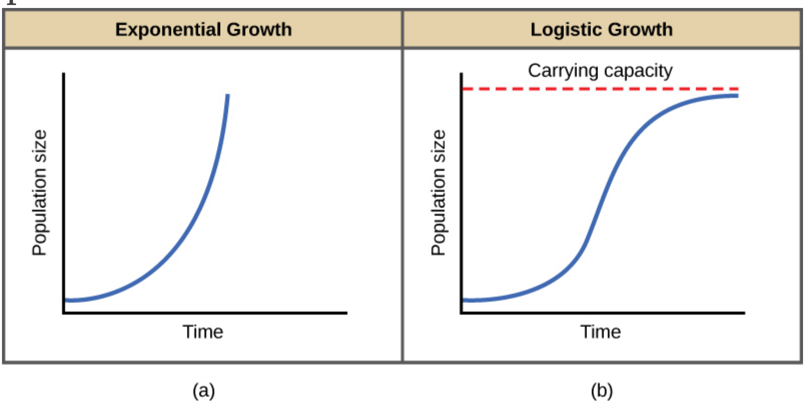
where there are few individuals and plentiful resources, but when the number of individuals gets large enough, resources will be depleted and the growth rate will slow down. Eventually, the growth rate will plateau or level off ([link]**b**). This population size, which is determined by the maximum population size that a particular environment can sustain, is called the **carrying capacity**, or *K*. In real populations, a growing population often overshoots its carrying capacity, and the death rate increases beyond the birth rate causing the population size to decline back to the carrying capacity or below it. Most populations usually fluctuate around the carrying capacity in an undulating fashion rather than existing right at it.

The formula used to calculate logistic growth adds the carrying capacity as a moderating force in the growth rate. The expression "*K* – *N*" is equal to the number of individuals that may be added to a population at a given time, and "*K* – *N*" divided by "*K*" is the fraction of the carrying capacity available for further growth. Thus, the exponential growth model is restricted by this factor to generate the logistic growth equation:

$$\text{Population growth} = rN \left[\frac{K-N}{K} \right]$$

Notice that when *N* is almost zero the quantity in brackets is almost equal to 1 (or *K*/*K*) and growth is close to exponential. When the population size is equal to the carrying capacity, or $N = K$, the

quantity in brackets is equal to zero and growth is equal to zero. A graph of this equation (logistic growth) yields the **S-shaped curve** ([link]**b**). It is a more realistic model of population growth than exponential growth. There are three different sections to an S-shaped curve. Initially, growth is exponential because there are few individuals and ample resources available. Then, as resources begin to become limited, the growth rate decreases. Finally, the growth rate levels off at the carrying capacity of the environment, with little change in population number over time.



Role of Intraspecific Competition

The logistic model assumes that every individual within a population will have equal access to resources and, thus, an equal chance for survival. For plants, the amount of water, sunlight, nutrients, and space to grow are the important resources, whereas in animals, important resources include food, water, shelter, nesting space, and mates.

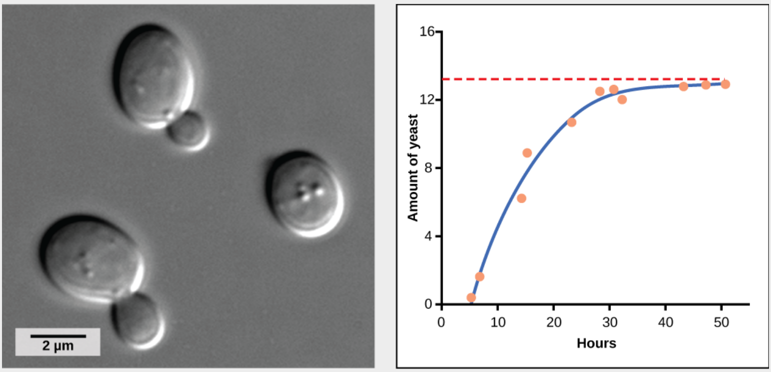
In the real world, phenotypic variation among individuals within a population means that some individuals will be better adapted to their environment than others. The resulting competition for resources among population members of the same species is termed **intraspecific competition**. Intraspecific competition may not affect populations that are well below their carrying capacity, as resources are plentiful and all individuals can obtain what they need. However, as population size increases, this competition intensifies. In addition, the accumulation of waste products can reduce carrying capacity in an environment.

Examples of Logistic Growth

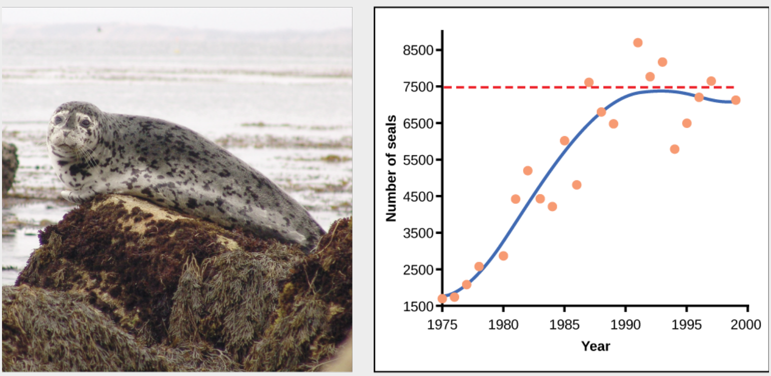
Yeast, a microscopic fungus used to make bread and alcoholic beverages, exhibits the classical S-shaped curve when grown in a test tube ([link]**a**). Its growth levels off as the population depletes the nutrients that are necessary for its growth. In the real world, however, there are variations to this idealized curve. Examples in wild populations include sheep and harbor seals ([link]**b**). In both examples, the population size exceeds the carrying capacity for short periods of time and then falls below the carrying capacity afterwards. This fluctuation in population size continues to occur as the population oscillates around its carrying capacity. Still, even with this oscillation, the logistic model is confirmed.

Visual Connection

(a) Yeast grown in ideal conditions in a test tube shows a classical S-shaped logistic growth curve, whereas (b) a natural population of seals shows real-world fluctuation. The yeast is visualized using differential interference contrast light micrography. (credit a: scale-bar data from Matt Russell)



(a)



(b)

If the major food source of seals declines due to pollution or overfishing, which of the following would likely occur?

1. The carrying capacity of seals would decrease, as would the seal population.

2. The carrying capacity of seals would decrease, but the seal population would remain the same.
3. The number of seal deaths would increase, but the number of births would also increase, so the population size would remain the same.
4. The carrying capacity of seals would remain the same, but the population of seals would decrease.

Population Dynamics and Regulation

The logistic model of population growth, while valid in many natural populations and a useful model, is a simplification of real-world population dynamics. Implicit in the model is that the carrying capacity of the environment does not change, which is not the case. The carrying capacity varies annually. For example, some summers are hot and dry whereas others are cold and wet; in many areas, the carrying capacity during the winter is much lower than it is during the summer. Also, natural events such as earthquakes, volcanoes, and fires can alter an environment and hence its carrying capacity. Additionally, populations do not usually exist in isolation. They share the environment with other species, competing with them for the same resources

(interspecific competition). These factors are also important to understanding how a specific population will grow.

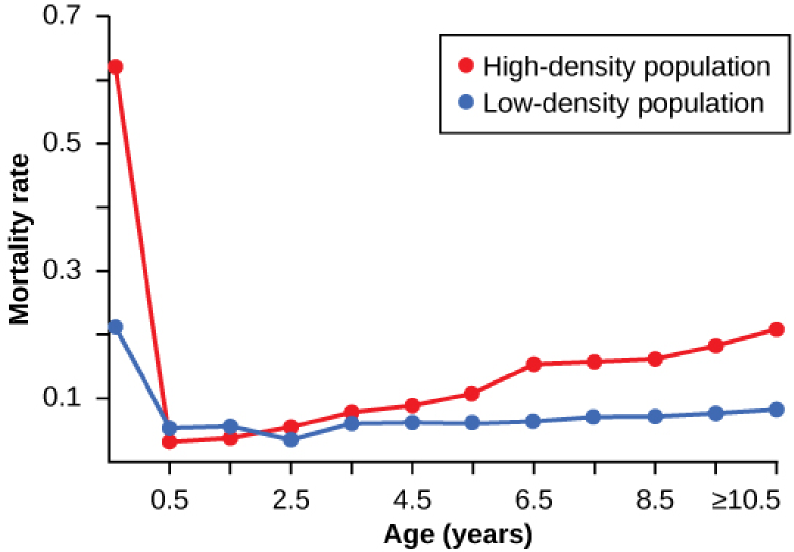
Population growth is regulated in a variety of ways. These are grouped into **density-dependent** factors, in which the density of the population affects growth rate and mortality, and **density-independent** factors, which cause mortality in a population regardless of population density. Wildlife biologists, in particular, want to understand both types because this helps them manage populations and prevent extinction or overpopulation.
David Choquenot, "Density-Dependent Growth, Body Condition, and Demography in Feral Donkeys: Testing the Food Hypothesis," *Ecology* 72, no. 3 (June 1991):805–813. This graph shows the age-specific mortality rates for wild donkeys from high- and low-density populations. The juvenile mortality is much higher in the high-density population because of maternal malnutrition caused by a shortage of high-quality food.

Density-dependent Regulation

Most density-dependent factors are biological in nature and include predation, inter- and intraspecific competition, and parasites. Usually, the denser a population is, the greater its mortality rate. For example, during intra- and interspecific competition, the reproductive rates of the species

will usually be lower, reducing their populations' rate of growth. In addition, low prey density increases the mortality of its predator because it has more difficulty locating its food source. Also, when the population is denser, diseases spread more rapidly among the members of the population, which affect the mortality rate.

Density dependent regulation was studied in a natural experiment with wild donkey populations on two sites in Australia.[footnote] On one site the population was reduced by a population control program; the population on the other site received no interference. The high-density plot was twice as dense as the low-density plot. From 1986 to 1987 the high-density plot saw no change in donkey density, while the low-density plot saw an increase in donkey density. The difference in the growth rates of the two populations was caused by mortality, not by a difference in birth rates. The researchers found that numbers of offspring birthed by each mother was unaffected by density. Growth rates in the two populations were different mostly because of juvenile mortality caused by the mother's malnutrition due to scarce high-quality food in the dense population. [link] shows the difference in age-specific mortalities in the two populations.



Density-independent Regulation and Interaction with Density-dependent Factors

Many factors that are typically physical in nature cause mortality of a population regardless of its density. These factors include weather, natural disasters, and pollution. An individual deer will be killed in a forest fire regardless of how many deer happen to be in that area. Its chances of survival are the same whether the population density is high or low. The same holds true for cold winter weather.

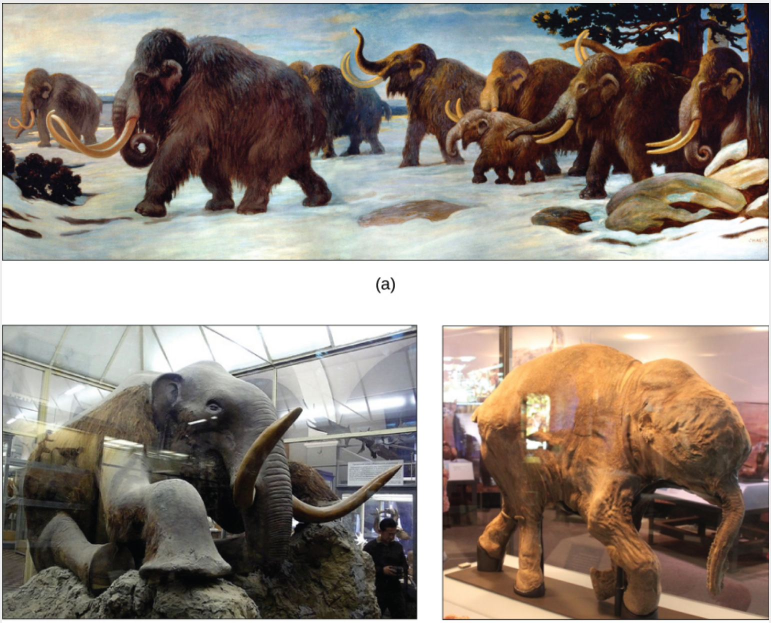
In real-life situations, population regulation is very complicated and density-dependent and independent factors can interact. A dense

population that suffers mortality from a density-independent cause will be able to recover differently than a sparse population. For example, a population of deer affected by a harsh winter will recover faster if there are more deer remaining to reproduce.

Evolution in Action

Why Did the Woolly Mammoth Go Extinct?

The three images include: (a) 1916 mural of a mammoth herd from the American Museum of Natural History, (b) the only stuffed mammoth in the world is in the Museum of Zoology located in St. Petersburg, Russia, and (c) a one-month-old baby mammoth, named Lyuba, discovered in Siberia in 2007. (credit a: modification of work by Charles R. Knight; credit b: modification of work by “Tanapon”/Flickr; credit c: modification of work by Matt Howry)



(a) (b) (c)

Woolly mammoths began to go extinct about 10,000 years ago, soon after paleontologists believe humans able to hunt them began to colonize North America and northern Eurasia ([link]). A mammoth population survived on Wrangel Island, in the East Siberian Sea, and was isolated from human contact until as recently as 1700 BC. We know a lot about these animals from carcasses found frozen in the ice of Siberia and other northern regions.

It is commonly thought that climate change and human hunting led to their extinction. A 2008 study estimated that climate change reduced the mammoth's range from 3,000,000 square miles 42,000 years ago to 310,000 square miles 6,000 years ago.[footnote] Through archaeological evidence of kill sites, it is also well documented that humans

hunted these animals. A 2012 study concluded that no single factor was exclusively responsible for the extinction of these magnificent creatures.[footnote] In addition to climate change and reduction of habitat, scientists demonstrated another important factor in the mammoth's extinction was the migration of human hunters across the Bering Strait to North America during the last ice age 20,000 years ago.

David Nogués-Bravo et al., "Climate Change, Humans, and the Extinction of the Woolly Mammoth." *PLoS Biol* 6 (April 2008): e79, doi:10.1371/journal.pbio.0060079.G.M. MacDonald et al., "Pattern of Extinction of the Woolly Mammoth in Beringia." *Nature Communications* 3, no. 893 (June 2012), doi:10.1038/ncomms1881.

The maintenance of stable populations was and is very complex, with many interacting factors determining the outcome. It is important to remember that humans are also part of nature. Once we contributed to a species' decline using primitive hunting technology only.

Demographic-Based Population Models

Population ecologists have hypothesized that suites

of characteristics may evolve in species that lead to particular adaptations to their environments. These adaptations impact the kind of population growth their species experience. Life history characteristics such as birth rates, age at first reproduction, the numbers of offspring, and even death rates evolve just like anatomy or behavior, leading to adaptations that affect population growth. Population ecologists have described a continuum of life-history "strategies" with *K*-selected species on one end and *r*-selected species on the other. ***K*-selected species** are adapted to stable, predictable environments. Populations of *K*-selected species tend to exist close to their carrying capacity. These species tend to have larger, but fewer, offspring and contribute large amounts of resources to each offspring. Elephants would be an example of a *K*-selected species. ***r*-selected species** are adapted to unstable and unpredictable environments. They have large numbers of small offspring. Animals that are *r*-selected do not provide a lot of resources or parental care to offspring, and the offspring are relatively self-sufficient at birth. Examples of *r*-selected species are marine invertebrates such as jellyfish and plants such as the dandelion. The two extreme strategies are at two ends of a continuum on which real species life histories will exist. In addition, life history strategies do not need to evolve as suites, but can evolve independently of each other, so each species may have some characteristics that trend toward one extreme or the

other.

Section Summary

Populations with unlimited resources grow exponentially—with an accelerating growth rate. When resources become limiting, populations follow a logistic growth curve in which population size will level off at the carrying capacity.

Populations are regulated by a variety of density-dependent and density-independent factors. Life-history characteristics, such as age at first reproduction or numbers of offspring, are characteristics that evolve in populations just as anatomy or behavior can evolve over time. The model of *r*- and *K*-selection suggests that characters, and possibly suites of characters, may evolve adaptations to population stability near the carrying capacity (*K*-selection) or rapid population growth and collapse (*r*-selection). Species will exhibit adaptations somewhere on a continuum between these two extremes.

Art Exercise

[link] If the major food source of seals declines

due to pollution or overfishing, which of the following would likely occur?

1. The carrying capacity of seals would decrease, as would the seal population.
2. The carrying capacity of seals would decrease, but the seal population would remain the same.
3. The number of seal deaths would increase, but the number of births would also increase, so the population size would remain the same.
4. The carrying capacity of seals would remain the same, but the population of seals would decrease.

[link] A: The carrying capacity of seals would decrease, as would the seal population.

Multiple Choice

Species with limited resources usually exhibit a(n) ______ growth curve.

1. logistic
2. logical
3. experimental

4. exponential

A

The maximum growth rate characteristic of a species is called its ______.

1. limit
2. carrying capacity
3. biotic potential
4. exponential growth pattern

C

The population size of a species capable of being supported by the environment is called its ______.

1. limit
2. carrying capacity
3. biotic potential
4. logistic growth pattern

B

Species that have many offspring at one time

are usually:

1. *r*-selected
2. *K*-selected
3. both *r*- and *K*-selected
4. not selected

A

A forest fire is an example of _____ regulation.

1. density-dependent
2. density-independent
3. *r*-selected
4. *K*-selected

B

Free Response

Describe the growth at various parts of the S-shaped curve of logistic growth.

In the first part of the curve, when few individuals of the species are present and

resources are plentiful, growth is exponential, similar to a J-shaped curve. Later, growth slows due to the species using up resources. Finally, the population levels off at the carrying capacity of the environment, and it is relatively stable over time.

Give an example of how density-dependent and density-independent factors might interact.

If a natural disaster such as a fire happened in the winter, when populations are low, it would have a greater effect on the overall population and its recovery than if the same disaster occurred during the summer, when population levels are high.

Glossary

birth rate
: the number of births within a population at a specific point in time

carrying capacity
: the maximum number of individuals of a population that can be supported by the limited resources of a habitat

death rate

the number of deaths within a population at a specific point in time

density-dependent regulation
: the regulation of population in which birth and death rates are dependent on population size

density-independent regulation
: the regulation of population in which the death rate is independent of the population size

exponential growth
: an accelerating growth pattern seen in populations where resources are not limiting

intraspecific competition
: the competition among members of the same species

J-shaped growth curve
: the shape of an exponential growth curve

K-selected species
: a species suited to stable environments that produce a few, relatively large offspring and provide parental care

logistic growth
: the leveling off of exponential growth due to limiting resources

r-selected species

a species suited to changing environments that produce many offspring and provide little or no parental care

S-shaped growth curve

the shape of a logistic growth curve

zero population growth

the steady population size where birth rates and death rates are equal

The Human Population

By the end of this section, you will be able to:

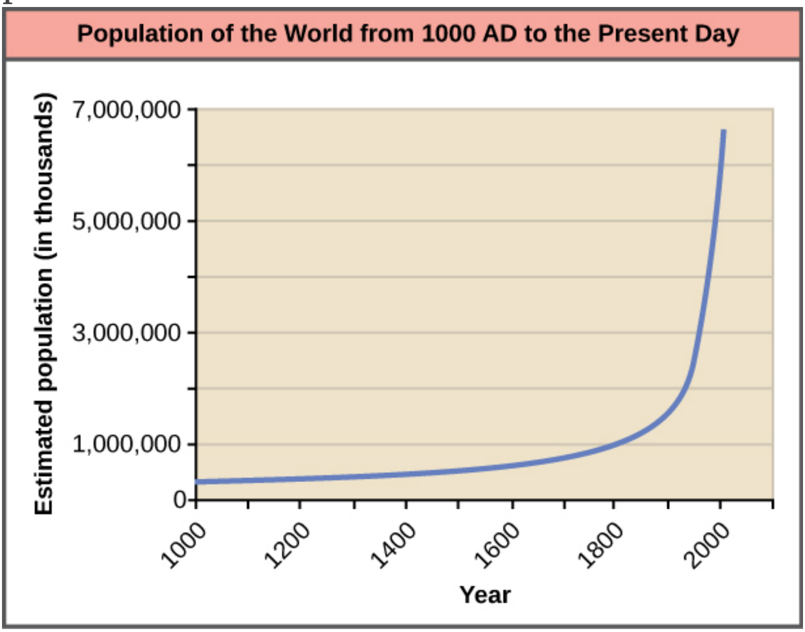
- Discuss how human population growth can be exponential
- Explain how humans have expanded the carrying capacity of their habitat
- Relate population growth and age structure to the level of economic development in different countries
- Discuss the long-term implications of unchecked human population growth

Concepts of animal population dynamics can be applied to human population growth. Humans are not unique in their ability to alter their environment. For example, beaver dams alter the stream environment where they are built. Humans, however, have the ability to alter their environment to increase its carrying capacity, sometimes to the detriment of other species. Earth's human population and their use of resources are growing rapidly, to the extent that some worry about the ability of Earth's environment to sustain its human population. Long-term exponential growth carries with it the potential risks of famine, disease, and large-scale death, as well as social consequences of crowding such as increased crime.

Human technology and particularly our harnessing of the energy contained in fossil fuels have caused

unprecedented changes to Earth's environment, altering ecosystems to the point where some may be in danger of collapse. Changes on a global scale including depletion of the ozone layer, desertification and topsoil loss, and global climate change are caused by human activities.

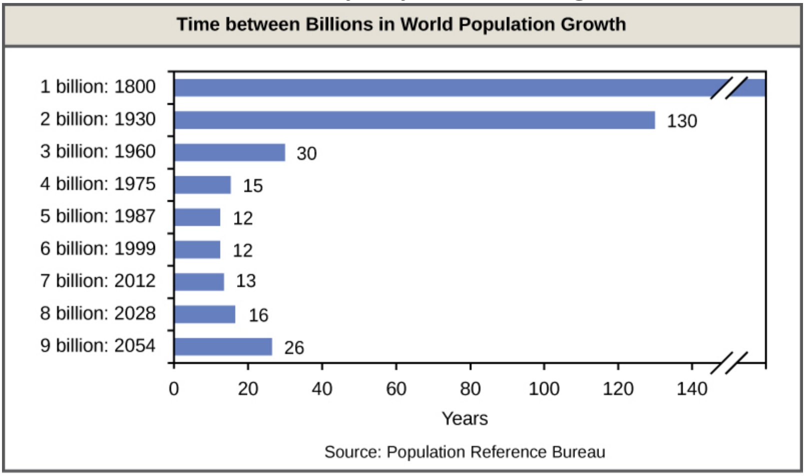
The world's human population is presently growing exponentially ([link]).
Human population growth since 1000 AD is exponential.



A consequence of exponential growth rate is that the time that it takes to add a particular number of humans to the population is becoming shorter. [link] shows that 123 years were necessary to add 1 billion humans between 1804 and 1930, but it only

took 24 years to add the two billion people between 1975 and 1999. This acceleration in growth rate will likely begin to decrease in the coming decades. Despite this, the population will continue to increase and the threat of overpopulation remains, particularly because the damage caused to ecosystems and biodiversity is lowering the human carrying capacity of the planet.

The time between the addition of each billion human beings to Earth decreases over time. (credit: modification of work by Ryan T. Cragun)



Concept in Action

Click through this video of how human populations have changed over time.

Danny Dorling, Mary Shaw, and George Davey

Smith, “Global Inequality of Life Expectancy due to AIDS,” *BMJ* 332, no. 7542 (March 2006): 662-664, doi: 10.1136/bmj.332.7542.662.

Overcoming Density-Dependent Regulation

Humans are unique in their ability to alter their environment in myriad ways. This ability is responsible for human population growth because it resets the carrying capacity and overcomes density-dependent growth regulation. Much of this ability is related to human intelligence, society, and communication. Humans construct shelters to protect themselves from the elements and have developed agriculture and domesticated animals to increase their food supplies. In addition, humans use language to communicate this technology to new generations, allowing them to improve upon previous accomplishments.

Other factors in human population growth are migration and public health. Humans originated in Africa, but we have since migrated to nearly all inhabitable land on Earth, thus, increasing the area that we have colonized. Public health, sanitation, and the use of antibiotics and vaccines have decreased the ability of infectious disease to limit human population growth in developed countries. In the past, diseases such as the bubonic plaque of the fourteenth century killed between 30 and 60

percent of Europe's population and reduced the overall world population by as many as one hundred million people. Infectious disease continues to have an impact on human population growth. For example, life expectancy in sub-Saharan Africa, which was increasing from 1950 to 1990, began to decline after 1985 largely as a result of HIV/AIDS mortality. The reduction in life expectancy caused by HIV/AIDS was estimated to be 7 years for 2005. [footnote]

Declining life expectancy is an indicator of higher mortality rates and leads to lower birth rates.

The fundamental cause of the acceleration of growth rate for humans in the past 200 years has been the reduced death rate due to a development of the technological advances of the industrial age, urbanization that supported those technologies, and especially the exploitation of the energy in fossil fuels. Fossil fuels are responsible for dramatically increasing the resources available for human population growth through agriculture (mechanization, pesticides, and fertilizers) and harvesting wild populations.

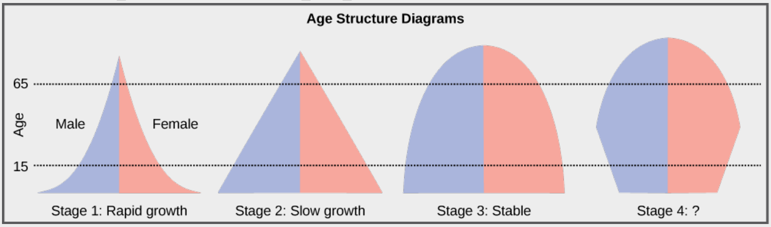
The percent growth rate of population in different countries is shown. Notice that the highest growth is occurring in less economically developed countries in Africa and Asia.

Age Structure, Population Growth, and Economic Development

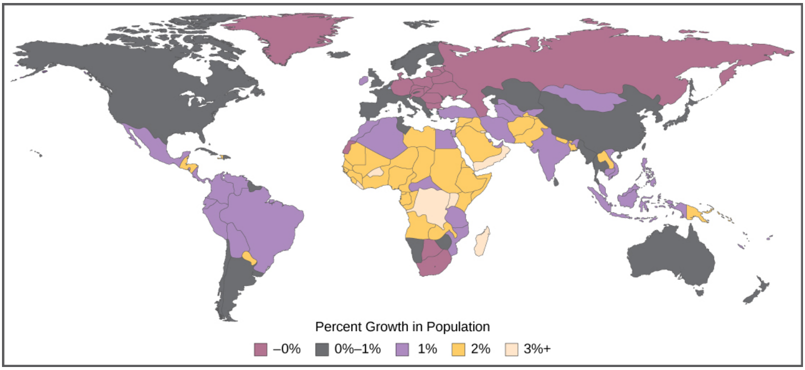
The age structure of a population is an important factor in population dynamics. **Age structure** is the proportion of a population in different age classes. Models that incorporate age structure allow better prediction of population growth, plus the ability to associate this growth with the level of economic development in a region. Countries with rapid growth have a pyramidal shape in their age structure diagrams, showing a preponderance of younger individuals, many of whom are of reproductive age ([link]). This pattern is most often observed in underdeveloped countries where individuals do not live to old age because of less-than-optimal living conditions, and there is a high birth rate. Age structures of areas with slow growth, including developed countries such as the United States, still have a pyramidal structure, but with many fewer young and reproductive-aged individuals and a greater proportion of older individuals. Other developed countries, such as Italy, have zero population growth. The age structure of these populations is more conical, with an even greater percentage of middle-aged and older individuals. The actual growth rates in different countries are shown in [link], with the highest rates tending to be in the less economically developed countries of Africa and Asia.

Visual Connection

Typical age structure diagrams are shown. The rapid growth diagram narrows to a point, indicating that the number of individuals decreases rapidly with age. In the slow growth model, the number of individuals decreases steadily with age. Stable population diagrams are rounded on the top, showing that the number of individuals per age group decreases gradually, and then increases for the older part of the population.



Age structure diagrams for rapidly growing, slow growing, and stable populations are shown in stages 1 through 3. What type of population change do you think stage 4 represents?



Paul R. Erlich, prologue to *The Population Bomb*, (1968; repr., New York: Ballantine, 1970).

Long-Term Consequences of Exponential Human Population Growth

Many dire predictions have been made about the world's population leading to a major crisis called the "population explosion." In the 1968 book *The Population Bomb*, biologist Dr. Paul R. Ehrlich wrote, "The battle to feed all of humanity is over. In the 1970s hundreds of millions of people will starve to death in spite of any crash programs embarked upon now. At this late date nothing can prevent a substantial increase in the world death rate."[footnote] While many critics view this statement as an exaggeration, the laws of exponential population growth are still in effect, and unchecked human population growth cannot continue indefinitely.

Efforts to moderate population control led to the **one-child policy** in China, which imposes fines on urban couples who have more than one child. Due to the fact that some couples wish to have a male heir, many Chinese couples continue to have more than one child. The effectiveness of the policy in limiting overall population growth is controversial, as is the policy itself. Moreover, there are stories of female infanticide having occurred in some of the more rural areas of the country. Family planning education programs in other countries have had highly positive effects on limiting population growth rates and increasing standards of living. In spite of population control policies, the human population

continues to grow. Because of the subsequent need to produce more and more food to feed our population, inequalities in access to food and other resources will continue to widen. The United Nations estimates the future world population size could vary from 6 billion (a decrease) to 16 billion people by the year 2100. There is no way to know whether human population growth will moderate to the point where the crisis described by Dr. Ehrlich will be averted.

Another consequence of population growth is the change and degradation of the natural environment. Many countries have attempted to reduce the human impact on climate change by limiting their emission of greenhouse gases. However, a global climate change treaty remains elusive, and many underdeveloped countries trying to improve their economic condition may be less likely to agree with such provisions without compensation if it means slowing their economic development. Furthermore, the role of human activity in causing climate change has become a hotly debated socio-political issue in some developed countries, including the United States. Thus, we enter the future with considerable uncertainty about our ability to curb human population growth and protect our environment to maintain the carrying capacity for the human species.

Concept in Action

Visit this website and select “Launch the movie” for an animation discussing the global impacts of human population growth.

Section Summary

Earth’s human population is growing exponentially. Humans have increased their carrying capacity through technology, urbanization, and harnessing the energy of fossil fuels. The age structure of a population allows us to predict population growth. Unchecked human population growth could have dire long-term effects on human welfare and Earth’s ecosystems.

Art Connections

[link] Age structure diagrams for rapidly growing, slow growing, and stable populations are shown in stages 1 through 3. What type of population change do you think stage 4 represents?

[link] Stage 4 represents a population that is decreasing.

Multiple Choice

A country with zero population growth is likely to be ______.

1. in Africa
2. in Asia
3. economically developed
4. economically underdeveloped

C

Which type of country has the greatest proportion of young individuals?

1. economically developed
2. economically underdeveloped
3. countries with zero population growth
4. countries in Europe

B

Which of the following is not a way that humans have increased the carrying capacity of the environment?

1. agriculture
2. using large amounts of natural resources
3. domestication of animals
4. use of language

B

Free Response

Describe the age structures in rapidly growing countries, slowly growing countries, and countries with zero population growth.

Rapidly growing countries have a large segment of the population at reproductive age or younger. Slower growing populations have a lower percentage of these individuals, and countries with zero population growth have an even lower percentage. On the other hand, a high proportion of older individuals is seen mostly in countries with zero growth, and a low proportion is most common in rapidly growing

countries.

Glossary

age structure
: the distribution of the proportion of population members in each age class

one-child policy
: a policy in China to limit population growth by limiting urban couples to have only one child or face a penalty of a fine

Community Ecology

By the end of this section, you will be able to:

- Discuss the predator-prey cycle
- Give examples of defenses against predation and herbivory
- Describe the competitive exclusion principle
- Give examples of symbiotic relationships between species
- Describe community structure and succession

Populations rarely, if ever, live in isolation from populations of other species. In most cases, numerous species share a habitat. The interactions between these populations play a major role in regulating population growth and abundance. All populations occupying the same habitat form a community: populations inhabiting a specific area at the same time. The number of species occupying the same habitat and their relative abundance is known as species diversity. Areas with low diversity, such as the glaciers of Antarctica, still contain a wide variety of living things, whereas the diversity of tropical rainforests is so great that it cannot be counted. Ecology is studied at the community level to understand how species interact with each other and compete for the same resources.

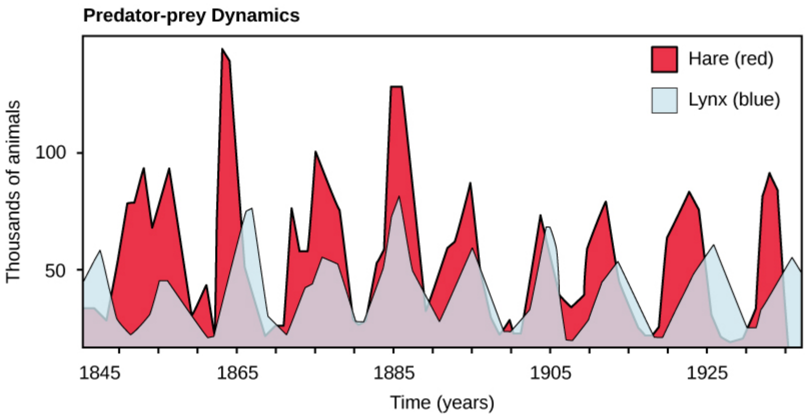
The cycling of lynx and snowshoe hare populations in Northern Ontario is an example of predator-prey dynamics. The (a) honey locust tree (*Gleditsia triacanthos*) uses thorns, a mechanical defense,

against herbivores, while the (b) Florida red-bellied turtle (*Pseudemys nelsoni)* uses its shell as a mechanical defense against predators. (c) Foxglove (*Digitalis* sp.) uses a chemical defense: toxins produced by the plant can cause nausea, vomiting, hallucinations, convulsions, or death when consumed. (d) The North American millipede (*Narceus americanus*) uses both mechanical and chemical defenses: when threatened, the millipede curls into a defensive ball and produces a noxious substance that irritates eyes and skin. (credit a: modification of work by Huw Williams; credit b: modification of work by “JamieS93”/Flickr; credit c: modification of work by Philip Jägenstedt; credit d: modification of work by Cory Zanker) (a) The tropical walking stick and (b) the chameleon use body shape and/or coloration to prevent detection by predators. (credit a: modification of work by Linda Tanner; credit b: modification of work by Frank Vassen) (a) The strawberry poison dart frog (*Oophaga pumilio*) uses aposematic coloration to warn predators that it is toxic, while the (b) striped skunk (*Mephitis mephitis*) uses aposematic coloration to warn predators of the unpleasant odor it produces. (credit a: modification of work by Jay Iwasaki; credit b: modification of work by Dan Dzurisin) Batesian mimicry occurs when a harmless species mimics the coloration of a harmful species, as is seen with the (a) bumblebee and (b) bee-like robber fly. (credit a, b: modification of work by Cory Zanker) Several unpleasant-tasting *Heliconius*

butterfly species share a similar color pattern with better-tasting varieties, an example of Müllerian mimicry. (credit: Joron M, Papa R, Beltrán M, Chamberlain N, Mavárez J, et al.)

Predation and Herbivory

Perhaps the classical example of species interaction is predation: the hunting of prey by its predator. Nature shows on television highlight the drama of one living organism killing another. Populations of predators and prey in a community are not constant over time: in most cases, they vary in cycles that appear to be related. The most often cited example of predator-prey dynamics is seen in the cycling of the lynx (predator) and the snowshoe hare (prey), using nearly 200 year-old trapping data from North American forests ([link]). This cycle of predator and prey lasts approximately 10 years, with the predator population lagging 1–2 years behind that of the prey population. As the hare numbers increase, there is more food available for the lynx, allowing the lynx population to increase as well. When the lynx population grows to a threshold level, however, they kill so many hares that hare population begins to decline, followed by a decline in the lynx population because of scarcity of food. When the lynx population is low, the hare population size begins to increase due, at least in part, to low predation pressure, starting the cycle anew.



The idea that the population cycling of the two species is entirely controlled by predation models has come under question. More recent studies have pointed to undefined density-dependent factors as being important in the cycling, in addition to predation. One possibility is that the cycling is inherent in the hare population due to density-dependent effects such as lower fecundity (maternal stress) caused by crowding when the hare population gets too dense. The hare cycling would then induce the cycling of the lynx because it is the lynxes' major food source. The more we study communities, the more complexities we find, allowing ecologists to derive more accurate and sophisticated models of population dynamics.

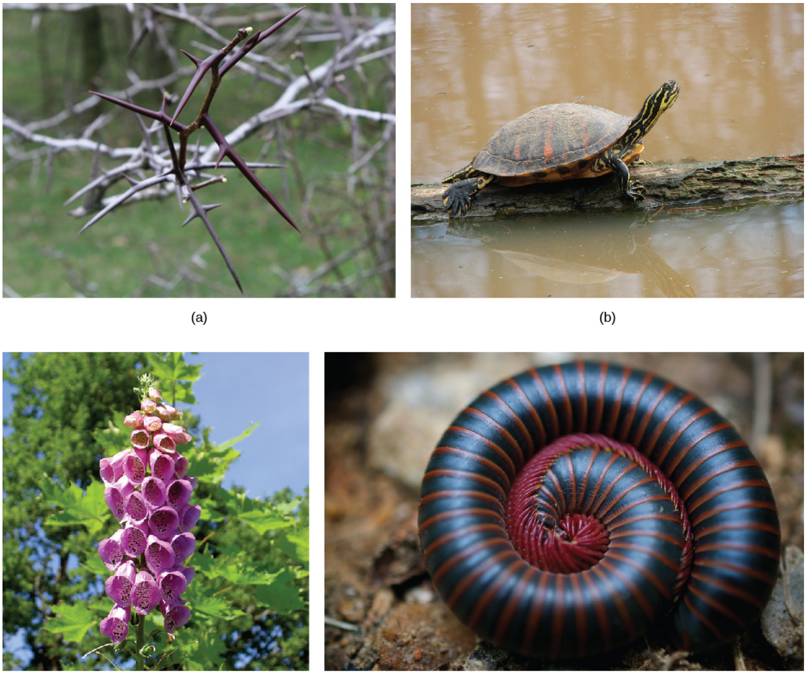
Herbivory describes the consumption of plants by insects and other animals, and it is another interspecific relationship that affects populations. Unlike animals, most plants cannot outrun predators or use mimicry to hide from hungry animals. Some

plants have developed mechanisms to defend against herbivory. Other species have developed mutualistic relationships; for example, herbivory provides a mechanism of seed distribution that aids in plant reproduction.

Defense Mechanisms against Predation and Herbivory

The study of communities must consider evolutionary forces that act on the members of the various populations contained within it. Species are not static, but slowly changing and adapting to their environment by natural selection and other evolutionary forces. Species have evolved numerous mechanisms to escape predation and herbivory. These defenses may be mechanical, chemical, physical, or behavioral.

Mechanical defenses, such as the presence of thorns on plants or the hard shell on turtles, discourage animal predation and herbivory by causing physical pain to the predator or by physically preventing the predator from being able to eat the prey. Chemical defenses are produced by many animals as well as plants, such as the foxglove which is extremely toxic when eaten. [link] shows some organisms' defenses against predation and herbivory.



(a) (b) (c) (d)

Many species use their body shape and coloration to avoid being detected by predators. The tropical walking stick is an insect with the coloration and body shape of a twig which makes it very hard to see when stationary against a background of real twigs ([link]**a**). In another example, the chameleon can change its color to match its surroundings ([link]**b**). Both of these are examples of **camouflage**, or avoiding detection by blending in with the background.


Some species use coloration as a way of warning predators that they are not good to eat. For example, the cinnabar moth caterpillar, the fire-bellied toad, and many species of beetle have bright colors that warn of a foul taste, the presence of toxic chemical, and/or the ability to sting or bite, respectively. Predators that ignore this coloration and eat the organisms will experience their unpleasant taste or presence of toxic chemicals and learn not to eat them in the future. This type of defensive mechanism is called **aposematic coloration**, or warning coloration ([link]).

(a) (b)

While some predators learn to avoid eating certain potential prey because of their coloration, other species have evolved mechanisms to mimic this coloration to avoid being eaten, even though they themselves may not be unpleasant to eat or contain toxic chemicals. In **Batesian mimicry**, a harmless species imitates the warning coloration of a harmful one. Assuming they share the same predators, this coloration then protects the harmless ones, even though they do not have the same level of physical or chemical defenses against predation as the organism they mimic. Many insect species mimic the coloration of wasps or bees, which are stinging, venomous insects, thereby discouraging predation ([link]).

In **Müllerian mimicry**, multiple species share the same warning coloration, but all of them actually have defenses. [link] shows a variety of foul-tasting butterflies with similar coloration. In **Emsleyan/ Mertensian mimicry**, a deadly prey mimics a less dangerous one, such as the venomous coral snake mimicking the non-venomous milk snake. This type of mimicry is extremely rare and more difficult to understand than the previous two types. For this type of mimicry to work, it is essential that eating

the milk snake has unpleasant but not fatal consequences. Then, these predators learn not to eat snakes with this coloration, protecting the coral snake as well. If the snake were fatal to the predator, there would be no opportunity for the predator to learn not to eat it, and the benefit for the less toxic species would disappear.

Link to Learning

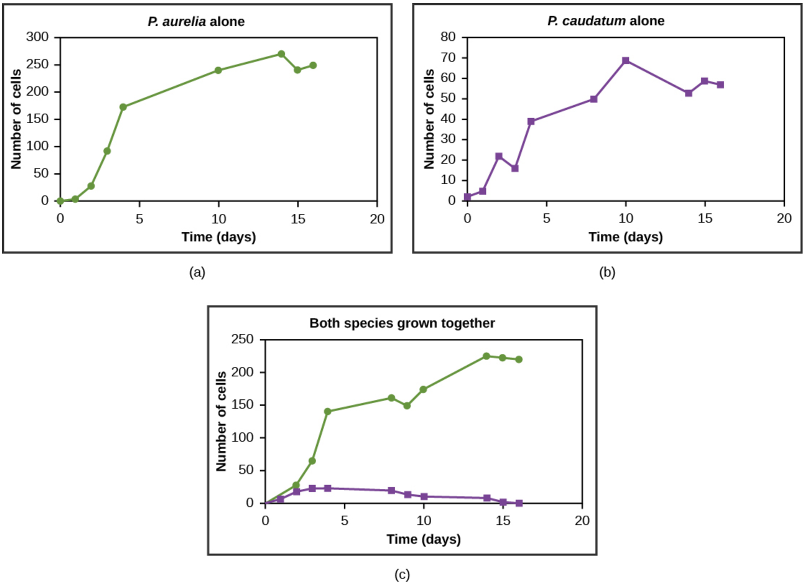
Go to this website to view stunning examples of mimicry.

Paramecium aurelia and *Paramecium caudatum* grow well individually, but when they compete for the same resources, the *P. aurelia* outcompetes the *P. caudatum*.

Competitive Exclusion Principle

Resources are often limited within a habitat and multiple species may compete to obtain them. All species have an ecological niche in the ecosystem, which describes how they acquire the resources they need and how they interact with other species in the community. The **competitive exclusion principle** states that two species cannot occupy the same niche in a habitat. In other words, different species cannot coexist in a community if they are competing for all the same resources. An example of this principle is shown in [link], with two protozoan species, *Paramecium aurelia* and *Paramecium caudatum*. When grown individually in the

laboratory, they both thrive. But when they are placed together in the same test tube (habitat), *P. aurelia* outcompetes *P. caudatum* for food, leading to the latter's eventual extinction.



This exclusion may be avoided if a population evolves to make use of a different resource, a different area of the habitat, or feeds during a different time of day, called resource partitioning. The two organisms are then said to occupy different microniches. These organisms coexist by minimizing direct competition.

The southern masked-weaver bird is starting to make a nest in a tree in Zambezi Valley, Zambia. This is an example of a commensal relationship, in which one species (the bird) benefits, while the other (the tree) neither benefits nor is harmed. (credit: "Hanay"/Wikimedia Commons) (a) Termites

form a mutualistic relationship with symbiotic protozoa in their guts, which allow both organisms to obtain energy from the cellulose the termite consumes. (b) Lichen is a fungus that has symbiotic photosynthetic algae living inside its cells. (credit a: modification of work by Scott Bauer, USDA; credit b: modification of work by Cory Zanker) This diagram shows the life cycle of a pork tapeworm (*Taenia solium*), a human worm parasite. (credit: modification of work by CDC)

Symbiosis

Symbiotic relationships, or **symbioses** (plural), are close interactions between individuals of different species over an extended period of time which impact the abundance and distribution of the associating populations. Most scientists accept this definition, but some restrict the term to only those species that are mutualistic, where both individuals benefit from the interaction. In this discussion, the broader definition will be used.

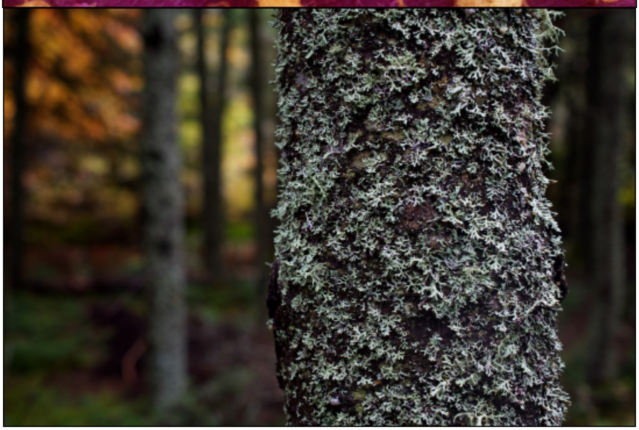
Commensalism

A **commensal** relationship occurs when one species benefits from the close, prolonged interaction, while the other neither benefits nor is harmed. Birds nesting in trees provide an example of a commensal relationship ([link]). The tree is not harmed by the

presence of the nest among its branches. The nests are light and produce little strain on the structural integrity of the branch, and most of the leaves, which the tree uses to get energy by photosynthesis, are above the nest so they are unaffected. The bird, on the other hand, benefits greatly. If the bird had to nest in the open, its eggs and young would be vulnerable to predators. Another example of a commensal relationship is the clown fish and the sea anemone. The sea anemone is not harmed by the fish, and the fish benefits with protection from predators who would be stung upon nearing the sea anemone.

Mutualism

A second type of symbiotic relationship is called **mutualism**, where two species benefit from their interaction. Some scientists believe that these are the only true examples of symbiosis. For example, termites have a mutualistic relationship with protozoa that live in the insect’s gut ([link]**a**). The termite benefits from the ability of bacterial symbionts within the protozoa to digest cellulose. The termite itself cannot do this, and without the protozoa, it would not be able to obtain energy from its food (cellulose from the wood it chews and eats). The protozoa and the bacterial symbionts benefit by having a protective environment and a constant supply of food from the wood chewing actions of the termite. Lichens have a mutualistic relationship between fungus and photosynthetic algae or bacteria ([link]**b**). As these symbionts grow together, the glucose produced by the algae provides nourishment for both organisms, whereas the physical structure of the lichen protects the algae from the elements and makes certain nutrients in the atmosphere more available to the algae.

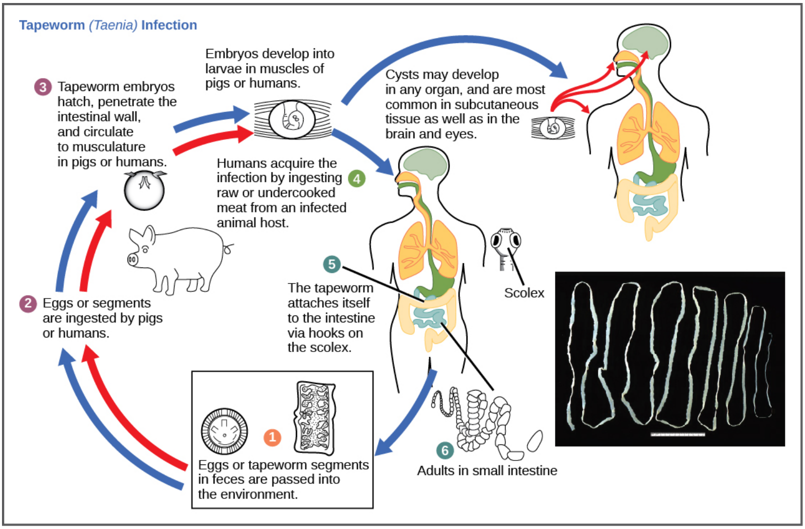


Parasitism

A **parasite** is an organism that lives in or on another living organism and derives nutrients from it. In this relationship, the parasite benefits, but the organism being fed upon, the **host** is harmed. The host is usually weakened by the parasite as it siphons resources the host would normally use to maintain itself. The parasite, however, is unlikely to kill the host, especially not quickly, because this would allow no time for the organism to complete its

reproductive cycle by spreading to another host.

The reproductive cycles of parasites are often very complex, sometimes requiring more than one host species. A tapeworm is a parasite that causes disease in humans when contaminated, undercooked meat such as pork, fish, or beef is consumed ([link]). The tapeworm can live inside the intestine of the host for several years, benefiting from the food the host is bringing into its gut by eating, and may grow to be over 50 ft long by adding segments. The parasite moves from species to species in a cycle, making two hosts necessary to complete its life cycle. Another common parasite is *Plasmodium falciparum*, the protozoan cause of malaria, a significant disease in many parts of the world. Living in human liver and red blood cells, the organism reproduces asexually in the gut of blood-feeding mosquitoes to complete its life cycle. Thus malaria is spread from human to human by mosquitoes, one of many arthropod-borne infectious diseases.



Coral is the foundation species of coral reef ecosystems. (credit: Jim E. Maragos, USFWS) The greatest species richness for mammals in North and South America is associated with the equatorial latitudes. (credit: modification of work by NASA, CIESIN, Columbia University) The *Pisaster ochraceus* sea star is a keystone species. (credit: Jerry Kirkhart)

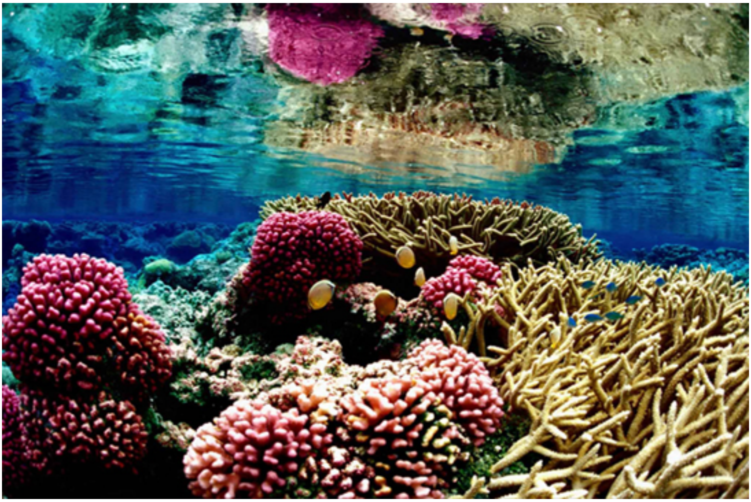
Characteristics of Communities

Communities are complex entities that can be characterized by their structure (the types and numbers of species present) and dynamics (how communities change over time). Understanding community structure and dynamics enables community ecologists to manage ecosystems more effectively.

Foundation Species

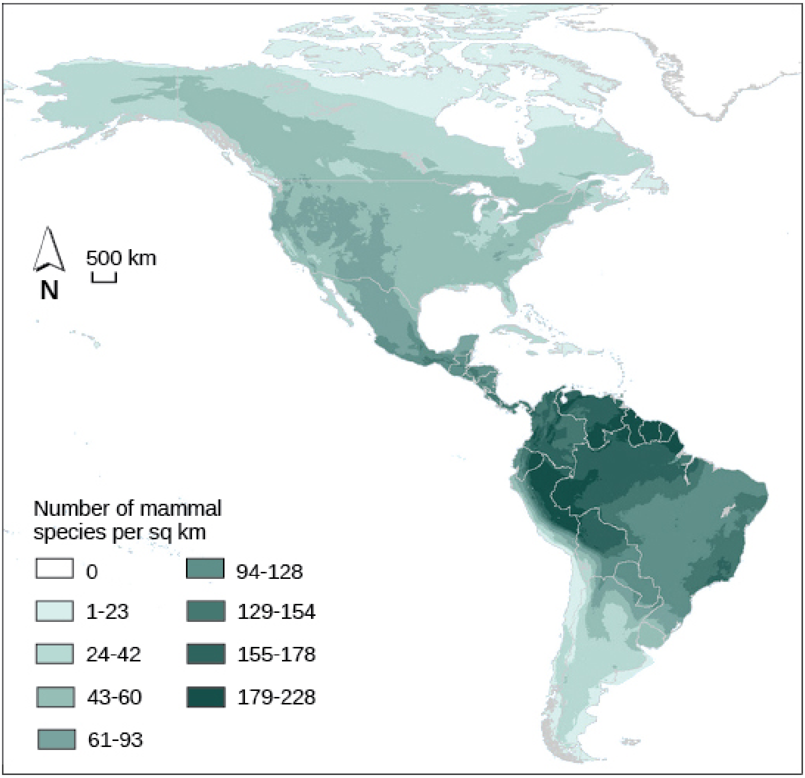
Foundation species are considered the "base" or "bedrock" of a community, having the greatest influence on its overall structure. They are usually the primary producers: organisms that bring most of the energy into the community. Kelp, brown algae, is a foundation species, forming the basis of the kelp forests off the coast of California.

Foundation species may physically modify the environment to produce and maintain habitats that benefit the other organisms that use them. An example is the photosynthetic corals of the coral reef ([link]). Corals themselves are not photosynthetic, but harbor symbionts within their body tissues (dinoflagellates called zooxanthellae) that perform photosynthesis; this is another example of a mutualism. The exoskeletons of living and dead coral make up most of the reef structure, which protects many other species from waves and ocean currents.



Biodiversity, Species Richness, and Relative Species Abundance

Biodiversity describes a community's biological complexity: it is measured by the number of different species (species richness) in a particular area and their relative abundance (species evenness). The area in question could be a habitat, a biome, or the entire biosphere. **Species richness** is the term that is used to describe the number of species living in a habitat or biome. Species richness varies across the globe ([link]). One factor in determining species richness is latitude, with the greatest species richness occurring in ecosystems near the equator, which often have warmer temperatures, large amounts of rainfall, and low seasonality. The lowest species richness occurs near the poles, which are much colder, drier, and thus less conducive to life in Geologic time (time since glaciations). The predictability of climate or productivity is also an important factor. Other factors influence species richness as well. For example, the study of **island biogeography** attempts to explain the relatively high species richness found in certain isolated island chains, including the Galápagos Islands that inspired the young Darwin. **Relative species abundance** is the number of individuals in a species relative to the total number of individuals in all species within a habitat, ecosystem, or biome. Foundation species often have the highest relative abundance of species.



Keystone Species

A **keystone species** is one whose presence is key to maintaining biodiversity within an ecosystem and to upholding an ecological community's structure. The intertidal sea star, *Pisaster ochraceus*, of the northwestern United States is a keystone species ([link]). Studies have shown that when this organism is removed from communities, populations of their natural prey (mussels) increase, completely altering the species composition and reducing biodiversity. Another keystone species is the banded tetra, a fish in tropical streams, which supplies

nearly all of the phosphorus, a necessary inorganic nutrient, to the rest of the community. If these fish were to become extinct, the community would be greatly affected.

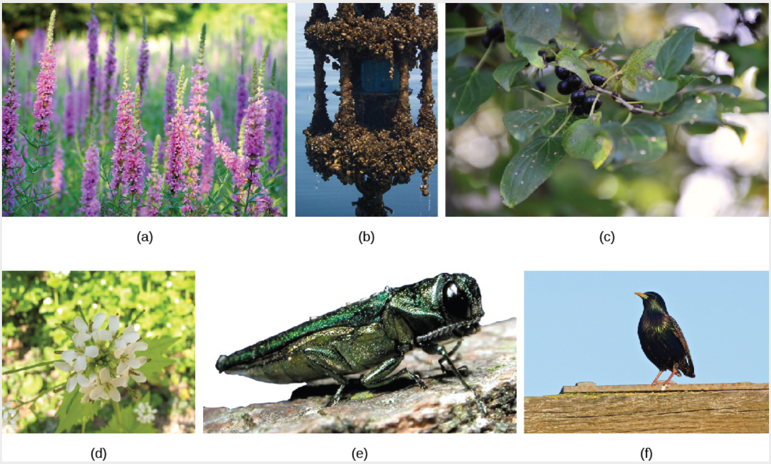
Everyday Connection

Invasive Species

Invasive species are non-native organisms that, when introduced to an area out of their native range, threaten the ecosystem balance of that habitat. Many such species exist in the United States, as shown in [link]. Whether enjoying a forest hike, taking a summer boat trip, or simply walking down an urban street, you have likely encountered an invasive species.

In the United States, invasive species like (a) purple loosestrife (*Lythrum salicaria*) and the (b) zebra mussel (*Dreissena polymorpha*) threaten

certain aquatic ecosystems. Some forests are threatened by the spread of (c) common buckthorn (*Rhamnus cathartica*), (d) garlic mustard (*Alliaria petiolata*), and (e) the emerald ash borer (*Agrilus planipennis*). The (f) European starling (*Sturnus vulgaris*) may compete with native bird species for nest holes. (credit a: modification of work by Liz West; credit b: modification of work by M. McCormick, NOAA; credit c: modification of work by E. Dronkert; credit d: modification of work by Dan Davison; credit e: modification of work by USDA; credit f: modification of work by Don DeBold)



One of the many recent proliferations of an invasive species concerns the growth of Asian carp populations. Asian carp were introduced to the United States in the 1970s by fisheries and sewage treatment facilities that used the fish's excellent filter feeding capabilities to clean their ponds of excess plankton. Some of the fish escaped, however, and by the 1980s they had colonized

many waterways of the Mississippi River basin, including the Illinois and Missouri Rivers. Voracious eaters and rapid reproducers, Asian carp may outcompete native species for food, potentially leading to their extinction. For example, black carp are voracious eaters of native mussels and snails, limiting this food source for native fish species. Silver carp eat plankton that native mussels and snails feed on, reducing this food source by a different alteration of the food web. In some areas of the Mississippi River, Asian carp species have become the most predominant, effectively outcompeting native fishes for habitat. In some parts of the Illinois River, Asian carp constitute 95 percent of the community's biomass. Although edible, the fish is bony and not a desired food in the United States. Moreover, their presence threatens the native fish and fisheries of the Great Lakes, which are important to local economies and recreational anglers. Asian carp have even injured humans. The fish, frightened by the sound of approaching motorboats, thrust themselves into the air, often landing in the boat or directly hitting the boaters.

The Great Lakes and their prized salmon and lake trout fisheries are also being threatened by these invasive fish. Asian carp have already colonized rivers and canals that lead into Lake Michigan. One infested waterway of particular importance is the Chicago Sanitary and Ship Channel, the major supply waterway linking the Great Lakes to the

Mississippi River. To prevent the Asian carp from leaving the canal, a series of electric barriers have been successfully used to discourage their migration; however, the threat is significant enough that several states and Canada have sued to have the Chicago channel permanently cut off from Lake Michigan. Local and national politicians have weighed in on how to solve the problem, but no one knows whether the Asian carp will ultimately be considered a nuisance, like other invasive species such as the water hyacinth and zebra mussel, or whether it will be the destroyer of the largest freshwater fishery of the world.

The issues associated with Asian carp show how population and community ecology, fisheries management, and politics intersect on issues of vital importance to the human food supply and economy. Socio-political issues like this make extensive use of the sciences of population ecology (the study of members of a particular species occupying a particular area known as a habitat) and community ecology (the study of the interaction of all species within a habitat).

During primary succession in lava on Maui, Hawaii, succulent plants are the pioneer species. (credit: Forest and Kim Starr) Secondary succession is shown in an oak and hickory forest after a forest fire.

Community Dynamics

Community dynamics are the changes in community structure and composition over time. Sometimes these changes are induced by **environmental disturbances** such as volcanoes, earthquakes, storms, fires, and climate change. Communities with a stable structure are said to be at equilibrium. Following a disturbance, the community may or may not return to the equilibrium state.

Succession describes the sequential appearance and disappearance of species in a community over time. In **primary succession**, newly exposed or newly formed land is colonized by living things; in **secondary succession**, part of an ecosystem is disturbed and remnants of the previous community remain.

Primary Succession and Pioneer Species

Primary succession occurs when new land is formed or rock is exposed: for example, following the eruption of volcanoes, such as those on the Big Island of Hawaii. As lava flows into the ocean, new land is continually being formed. On the Big Island, approximately 32 acres of land is added each year. First, weathering and other natural forces break down the substrate enough for the establishment of certain hearty plants and lichens with few soil requirements, known as **pioneer species** ([link]).

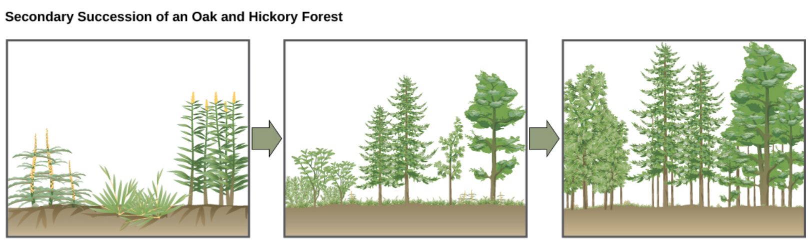
These species help to further break down the mineral rich lava into soil where other, less hardy species will grow and eventually replace the pioneer species. In addition, as these early species grow and die, they add to an ever-growing layer of decomposing organic material and contribute to soil formation. Over time the area will reach an equilibrium state, with a set of organisms quite different from the pioneer species.

Secondary succession

A classic example of secondary succession occurs in oak and hickory forests cleared by wildfire ([link]). Wildfires will burn most vegetation and kill those animals unable to flee the area. Their nutrients, however, are returned to the ground in the form of ash. Thus, even when areas are devoid of life due to severe fires, the area will soon be ready for new life

to take hold.

Before the fire, the vegetation was dominated by tall trees with access to the major plant energy resource: sunlight. Their height gave them access to sunlight while also shading the ground and other low-lying species. After the fire, though, these trees are no longer dominant. Thus, the first plants to grow back are usually annual plants followed within a few years by quickly growing and spreading grasses and other pioneer species. Due to, at least in part, changes in the environment brought on by the growth of the grasses and other species, over many years, shrubs will emerge along with small pine, oak, and hickory trees. These organisms are called intermediate species. Eventually, over 150 years, the forest will reach its equilibrium point where species composition is no longer changing and resembles the community before the fire. This equilibrium state is referred to as the **climax community**, which will remain stable until the next disturbance.



Pioneer species
Annual plants grow and are succeeded by grasses and perennials.

Intermediate species
Shrubs, then pines, and young oak and hickory begin to grow.

Climax community
The mature oak and hickory forest remains stable until the next disturbance.

Section Summary

Communities include all the different species living in a given area. The variety of these species is called species richness. Many organisms have developed defenses against predation and herbivory, including mechanical defenses, warning coloration, and mimicry, as a result of evolution and the interaction with other members of the community. Two species cannot exist in the same habitat competing directly for the same resources. Species may form symbiotic relationships such as commensalism or mutualism. Community structure is described by its foundation and keystone species. Communities respond to environmental disturbances by succession (the predictable appearance of different types of plant species) until a stable community structure is established.

Review Questions

The first species to live on new land, such as that formed from volcanic lava, are called _____.

1. climax community
2. keystone species
3. foundation species
4. pioneer species

D

Which type of mimicry involves multiple species with similar warning coloration that are all toxic to predators?

1. Batesian mimicry
2. Müllerian mimicry
3. Emsleyan/Mertensian mimicry
4. Mertensian mimicry

B

A symbiotic relationship where both of the coexisting species benefit from the interaction is called ______.

1. commensalism
2. parasitism
3. mutualism
4. communism

C

Free Response

Describe the competitive exclusion principle and its effects on competing species.

The competitive exclusion principle states that no two species competing for the same resources at the same time and place can coexist over time. Thus, one of the competing species will eventually dominate. On the other hand, if the species evolve such that they use resources from different parts of the habitat or at different times of day, the two species can exist together indefinitely.

Glossary

aposematic coloration
: warning coloration used as a defensive mechanism against predation

Batesian mimicry
: type of mimicry where a non-harmful species takes on the warning colorations of a harmful one

camouflage
: avoid detection by blending in with the background.

climax community
: final stage of succession, where a stable

community is formed by a characteristic assortment of plant and animal species

commensalism
: relationship between species wherein one species benefits from the close, prolonged interaction, while the other species neither benefits nor is harmed

competitive exclusion principle
: no two species within a habitat can coexist when they compete for the same resources at the same place and time

Emsleyan/Mertensian mimicry
: type of mimicry where a harmful species resembles a less harmful one

environmental disturbance
: change in the environment caused by natural disasters or human activities

foundation species
: species which often forms the major structural portion of the habitat

host
: organism a parasite lives on

island biogeography
: study of life on island chains and how their geography interacts with the diversity of

species found there

keystone species
: species whose presence is key to maintaining biodiversity in an ecosystem and to upholding an ecological community's structure

Müllerian mimicry
: type of mimicry where species share warning coloration and all are harmful to predators

mutualism
: symbiotic relationship between two species where both species benefit

parasite
: organism that uses resources from another species, the host

pioneer species
: first species to appear in primary and secondary succession

primary succession
: succession on land that previously has had no life

relative species abundance
: absolute population size of a particular species relative to the population sizes of other species within the community

secondary succession

succession in response to environmental disturbances that move a community away from its equilibrium

species richness
: number of different species in a community

symbiosis
: close interaction between individuals of different species over an extended period of time that impacts the abundance and distribution of the associating populations

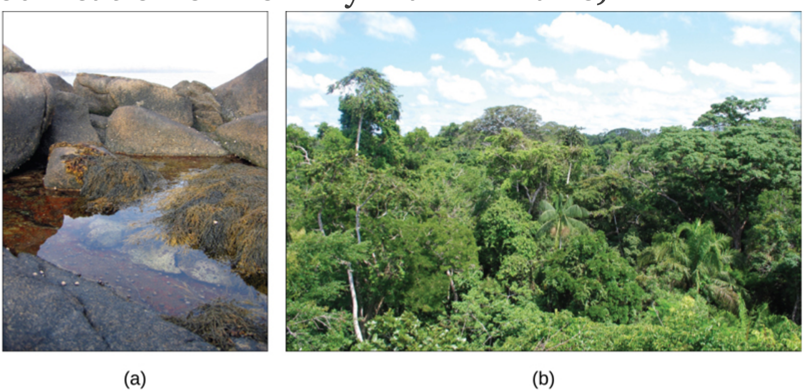
Ecology of Ecosystems

By the end of this section, you will be able to:

- Describe the basic types of ecosystems on Earth
- Differentiate between food chains and food webs and recognize the importance of each
- Describe how organisms acquire energy in a food web and in associated food chains
- Explain how the efficiency of energy transfers between trophic levels effects ecosystem

An **ecosystem** is a community of living organisms and their abiotic (non-living) environment. Ecosystems can be small, such as the tide pools found near the rocky shores of many oceans, or large, such as those found in the tropical rainforest of the Amazon in Brazil ([link]).

A (a) tidal pool ecosystem in Matinicus Island, Maine, is a small ecosystem, while the (b) Amazon rainforest in Brazil is a large ecosystem. (credit a: modification of work by Jim Kuhn; credit b: modification of work by Ivan Mlinaric)



There are three broad categories of ecosystems based on their general environment: freshwater, marine, and terrestrial. Within these three categories are individual ecosystem types based on the environmental habitat and organisms present. Desert ecosystems, like all ecosystems, can vary greatly. The desert in (a) Saguaro National Park, Arizona, has abundant plant life, while the rocky desert of (b) Boa Vista island, Cape Verde, Africa, is devoid of plant life. (credit a: modification of work by Jay Galvin; credit b: modification of work by Ingo Wölbern)

Ecology of Ecosystems

Life in an ecosystem often involves competition for limited resources, which occurs both within a single species and between different species. Organisms compete for food, water, sunlight, space, and mineral nutrients. These resources provide the energy for metabolic processes and the matter to make up organisms' physical structures. Other critical factors influencing community dynamics are the components of its physical environment: a habitat's climate (seasons, sunlight, and rainfall), elevation, and geology. These can all be important environmental variables that determine which organisms can exist within a particular area.

Freshwater ecosystems are the least common, occurring on only 1.8 percent of Earth's surface.

These systems comprise lakes, rivers, streams, and springs; they are quite diverse, and support a variety of animals, plants, fungi, protists and prokaryotes.

Marine ecosystems are the most common, comprising 75 percent of Earth's surface and consisting of three basic types: shallow ocean, deep ocean water, and deep ocean bottom. Shallow ocean ecosystems include extremely biodiverse coral reef ecosystems, yet the deep ocean water is known for large numbers of plankton and krill (small crustaceans) that support it. These two environments are especially important to aerobic respirators worldwide, as the phytoplankton perform 40 percent of all photosynthesis on Earth. Although not as diverse as the other two, deep ocean bottom ecosystems contain a wide variety of marine organisms. Such ecosystems exist even at depths where light is unable to penetrate through the water.

Terrestrial ecosystems, also known for their diversity, are grouped into large categories called biomes. A **biome** is a large-scale community of organisms, primarily defined on land by the dominant plant types that exist in geographic regions of the planet with similar climatic conditions. Examples of biomes include tropical rainforests, savannas, deserts, grasslands, temperate forests, and tundras. Grouping these ecosystems into just a few biome categories obscures the great

diversity of the individual ecosystems within them. For example, the saguaro cacti (*Carnegiea gigantean*) and other plant life in the Sonoran Desert, in the United States, are relatively diverse compared with the desolate rocky desert of Boa Vista, an island off the coast of Western Africa ([link]).

(a) (b)

Ecosystems and Disturbance

Ecosystems are complex with many interacting parts. They are routinely exposed to various disturbances: changes in the environment that affect their compositions, such as yearly variations in rainfall and temperature. Many disturbances are a result of natural processes. For example, when lightning causes a forest fire and destroys part of a forest ecosystem, the ground is eventually populated with grasses, followed by bushes and shrubs, and later mature trees: thus, the forest is restored to its former state. This process is so universal that ecologists have given it a name—succession. The impact of environmental disturbances caused by human activities is now as significant as the changes wrought by natural processes. Human agricultural

practices, air pollution, acid rain, global deforestation, overfishing, oil spills, and illegal dumping on land and into the ocean all have impacts on ecosystems.

Equilibrium is a dynamic state of an ecosystem in which, despite changes in species numbers and occurrence, biodiversity remains somewhat constant. In ecology, two parameters are used to measure changes in ecosystems: resistance and resilience. The ability of an ecosystem to remain at equilibrium in spite of disturbances is called **resistance**. The speed at which an ecosystem recovers equilibrium after being disturbed is called **resilience**. Ecosystem resistance and resilience are especially important when considering human impact. The nature of an ecosystem may change to such a degree that it can lose its resilience entirely. This process can lead to the complete destruction or irreversible altering of the ecosystem.

These are the trophic levels of a food chain in Lake Ontario at the United States–Canada border. Energy and nutrients flow from photosynthetic green algae at the base to the top of the food chain: the Chinook salmon. (credit: modification of work by National Oceanic and Atmospheric Administration/NOAA)
The relative energy in trophic levels in a Silver Springs, Florida, ecosystem is shown. Each trophic level has less energy available, and usually, but not always, supports a smaller mass of organisms at the next level. This food web shows the interactions

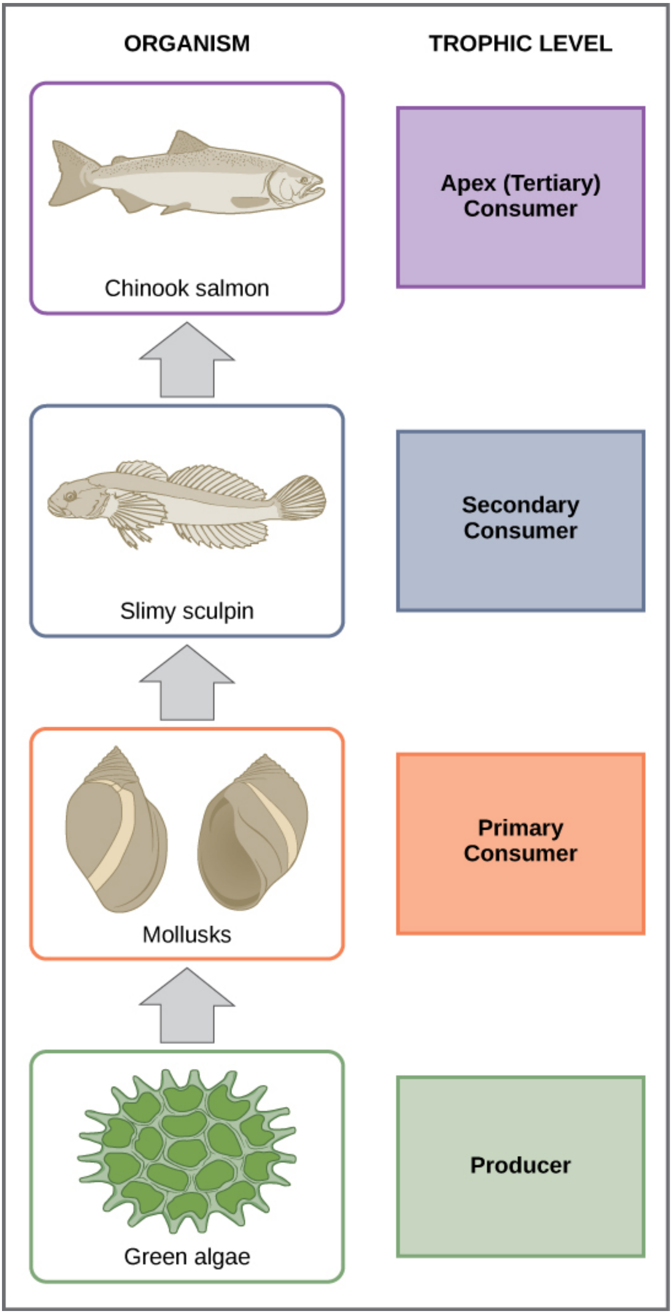
between organisms across trophic levels. Arrows point from an organism that is consumed to the organism that consumes it. All the producers and consumers eventually become nourishment for the decomposers (fungi, mold, earthworms, and bacteria in the soil). (credit "fox": modification of work by Kevin Bacher, NPS; credit "owl": modification of work by John and Karen Hollingsworth, USFWS; credit "snake": modification of work by Steve Jurvetson; credit "robin": modification of work by Alan Vernon; credit "frog": modification of work by Alessandro Catenazzi; credit "spider": modification of work by "Sanba38"/Wikimedia Commons; credit "centipede": modification of work by “Bauerph”/ Wikimedia Commons; credit "squirrel": modification of work by Dawn Huczek; credit "mouse": modification of work by NIGMS, NIH; credit "sparrow": modification of work by David Friel; credit "beetle": modification of work by Scott Bauer, USDA Agricultural Research Service; credit "mushrooms": modification of work by Chris Wee; credit "mold": modification of work by Dr. Lucille Georg, CDC; credit "earthworm": modification of work by Rob Hille; credit "bacteria": modification of work by Don Stalons, CDC)

Food Chains and Food Webs

A **food chain** is a linear sequence of organisms through which nutrients and energy pass as one organism eats another; the levels in the food chain

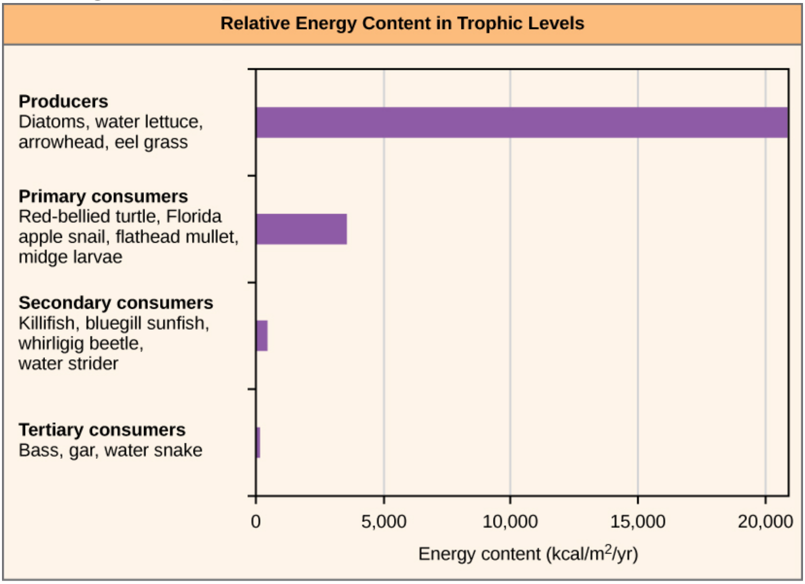
are producers, primary consumers, higher-level consumers, and finally decomposers. These levels are used to describe ecosystem structure and dynamics. There is a single path through a food chain. Each organism in a food chain occupies a specific **trophic level** (energy level), its position in the food chain or food web.

In many ecosystems, the base, or foundation, of the food chain consists of photosynthetic organisms (plants or phytoplankton), which are called **producers**. The organisms that consume the producers are herbivores: the **primary consumers**. **Secondary consumers** are usually carnivores that eat the primary consumers. **Tertiary consumers** are carnivores that eat other carnivores. Higher-level consumers feed on the next lower trophic levels, and so on, up to the organisms at the top of the food chain: the **apex consumers**. In the Lake Ontario food chain, shown in [link], the Chinook salmon is the apex consumer at the top of this food chain.



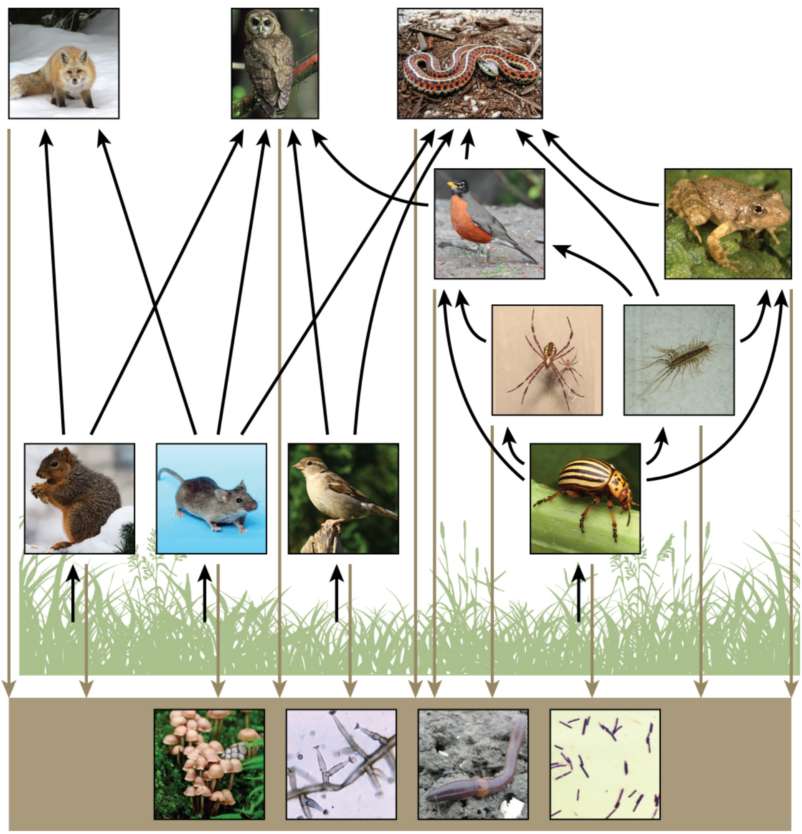
One major factor that limits the number of steps in a

food chain is energy. Energy is lost at each trophic level and between trophic levels as heat and in the transfer to decomposers ([link]). Thus, after a limited number of trophic energy transfers, the amount of energy remaining in the food chain may not be great enough to support viable populations at yet a higher trophic level.



There is a one problem when using food chains to describe most ecosystems. Even when all organisms are grouped into appropriate trophic levels, some of these organisms can feed on more than one trophic level; likewise, some of these organisms can also be fed on from multiple trophic levels. In addition, species feed on and are eaten by more than one species. In other words, the linear model of ecosystems, the food chain, is a hypothetical, overly simplistic representation of ecosystem structure. A

holistic model—which includes all the interactions between different species and their complex interconnected relationships with each other and with the environment—is a more accurate and descriptive model for ecosystems. A **food web** is a concept that accounts for the multiple trophic (feeding) interactions between each species and the many species it may feed on, or that feed on it. In a food web, the several trophic connections between each species and the other species that interact with it may cross multiple trophic levels. The matter and energy movements of virtually all ecosystems are more accurately described by food webs ([link]).



Concept in Action

Head to this online interactive simulator to investigate food web function. In the *Interactive Labs* box, under Food Web, click **Step 1**. Read the instructions first, and then click **Step 2** for additional instructions. When you are ready to create a simulation, in the upper-right corner of the *Interactive Labs* box, click **OPEN SIMULATOR**.

Two general types of food webs are often shown interacting within a single ecosystem. A **grazing food web** has plants or other photosynthetic organisms at its base, followed by herbivores and various carnivores. A **detrital food web** consists of a base of organisms that feed on decaying organic matter (dead organisms), including decomposers (which break down dead and decaying organisms) and detritivores (which consume organic detritus). These organisms are usually bacteria, fungi, and invertebrate animals that recycle organic material back into the biotic part of the ecosystem as they themselves are consumed by other organisms. As ecosystems require a method to recycle material from dead organisms, grazing food webs have an associated detrital food web. For example, in a meadow ecosystem, plants may support a grazing food web of different organisms, primary and other levels of consumers, while at the same time supporting a detrital food web of bacteria and fungi

feeding off dead plants and animals. Simultaneously, a detrital food web can contribute energy to a grazing food web, as when a robin eats an earthworm.

Swimming shrimp, a few squat lobsters, and hundreds of vent mussels are seen at a hydrothermal vent at the bottom of the ocean. As no sunlight penetrates to this depth, the ecosystem is supported by chemoautotrophic bacteria and organic material that sinks from the ocean's surface. This picture was taken in 2006 at the submerged NW Eifuku volcano off the coast of Japan by the National Oceanic and Atmospheric Administration (NOAA). The summit of this highly active volcano lies 1535 m below the surface.

How Organisms Acquire Energy in a Food Web

All living things require energy in one form or another. Energy is used by most complex metabolic pathways (usually in the form of ATP), especially those responsible for building large molecules from smaller compounds. Living organisms would not be able to assemble macromolecules (proteins, lipids, nucleic acids, and complex carbohydrates) from their monomers without a constant energy input.

Food-web diagrams illustrate how energy flows directionally through ecosystems. They can also indicate how efficiently organisms acquire energy,

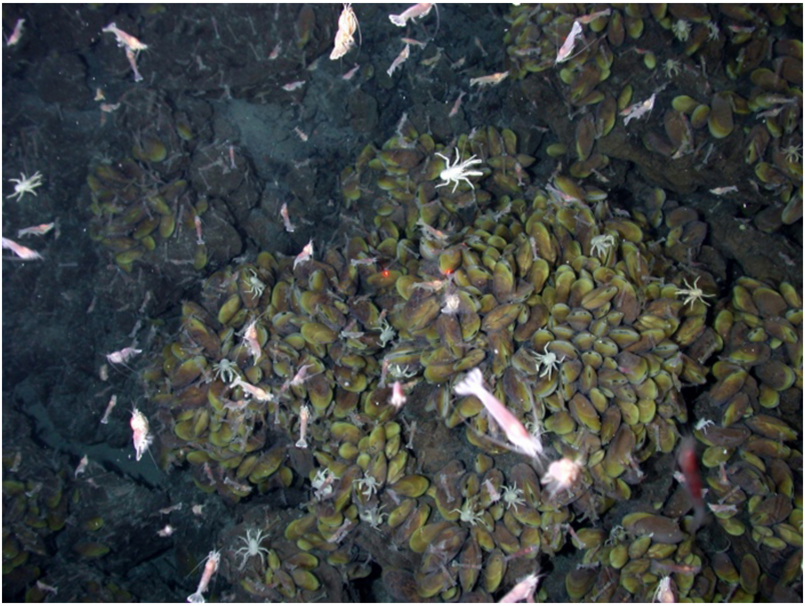
use it, and how much remains for use by other organisms of the food web. Energy is acquired by living things in two ways: autotrophs harness light or chemical energy and heterotrophs acquire energy through the consumption and digestion of other living or previously living organisms.

Photosynthetic and chemosynthetic organisms are **autotrophs**, which are organisms capable of synthesizing their own food (more specifically, capable of using inorganic carbon as a carbon source). Photosynthetic autotrophs (**photoautotrophs**) use sunlight as an energy source, and chemosynthetic autotrophs (**chemoautotrophs**) use inorganic molecules as an energy source. Autotrophs are critical for most ecosystems: they are the producer trophic level. Without these organisms, energy would not be available to other living organisms, and life itself would not be possible.

Photoautotrophs, such as plants, algae, and photosynthetic bacteria, are the energy source for a majority of the world's ecosystems. These ecosystems are often described by grazing and detrital food webs. Photoautotrophs harness the Sun's solar energy by converting it to chemical energy in the form of ATP (and NADP). The energy stored in ATP is used to synthesize complex organic molecules, such as glucose. The rate at which photosynthetic producers incorporate energy from

the Sun is called **gross primary productivity**. However, not all of the energy incorporated by producers is available to the other organisms in the food web because producers must also grow and reproduce, which consumes energy. **Net primary productivity** is the energy that remains in the producers after accounting for these organisms' respiration and heat loss. The net productivity is then available to the primary consumers at the next trophic level.

Chemoautotrophs are primarily bacteria and archaea that are found in rare ecosystems where sunlight is not available, such as those associated with dark caves or hydrothermal vents at the bottom of the ocean ([link]). Many chemoautotrophs in hydrothermal vents use hydrogen sulfide (H_2S), which is released from the vents as a source of chemical energy; this allows them to synthesize complex organic molecules, such as glucose, for their own energy and, in turn, supplies energy to the rest of the ecosystem.



This chart shows the PCB concentrations found at the various trophic levels in the Saginaw Bay ecosystem of Lake Huron. Notice that the fish in the higher trophic levels accumulate more PCBs than those in lower trophic levels. (credit: Patricia Van Hoof, NOAA)

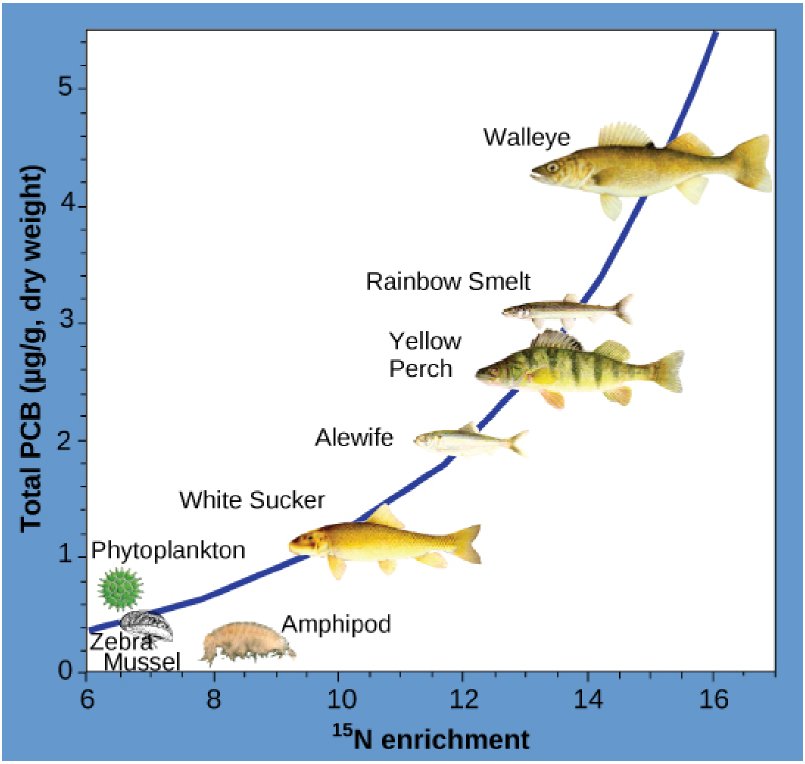
Consequences of Food Webs: Biological Magnification

One of the most important consequences of ecosystem dynamics in terms of human impact is biomagnification. **Biomagnification** is the increasing concentration of persistent, toxic substances in organisms at each successive trophic level. These are substances that are fat soluble, not water soluble, and are stored in the fat reserves of

each organism. Many substances have been shown to biomagnify, including classical studies with the pesticide dichlorodiphenyltrichloroethane (DDT), which were described in the 1960s bestseller, *Silent Spring* by Rachel Carson. DDT was a commonly used pesticide before its dangers to apex consumers, such as the bald eagle, became known. In aquatic ecosystems, organisms from each trophic level consumed many organisms in the lower level, which caused DDT to increase in birds (apex consumers) that ate fish. Thus, the birds accumulated sufficient amounts of DDT to cause fragility in their eggshells. This effect increased egg breakage during nesting and was shown to have devastating effects on these bird populations. The use of DDT was banned in the United States in the 1970s.

Other substances that biomagnify are polychlorinated biphenyls (PCB), which were used as coolant liquids in the United States until their use was banned in 1979, and heavy metals, such as mercury, lead, and cadmium. These substances are best studied in aquatic ecosystems, where predatory fish species accumulate very high concentrations of toxic substances that are at quite low concentrations in the environment and in producers. As illustrated in a study performed by the NOAA in the Saginaw Bay of Lake Huron of the North American Great Lakes ([link]), PCB concentrations increased from the producers of the ecosystem (phytoplankton) through the different trophic levels of fish species.

The apex consumer, the walleye, has more than four times the amount of PCBs compared to phytoplankton. Also, based on results from other studies, birds that eat these fish may have PCB levels at least one order of magnitude higher than those found in the lake fish.



Other concerns have been raised by the biomagnification of heavy metals, such as mercury and cadmium, in certain types of seafood. The United States Environmental Protection Agency recommends that pregnant women and young children should not consume any swordfish, shark, king mackerel, or tilefish because of their high

mercury content. These individuals are advised to eat fish low in mercury: salmon, shrimp, pollock, and catfish. Biomagnification is a good example of how ecosystem dynamics can affect our everyday lives, even influencing the food we eat.

Section Summary

Ecosystems exist underground, on land, at sea, and in the air. Organisms in an ecosystem acquire energy in a variety of ways, which is transferred between trophic levels as the energy flows from the base to the top of the food web, with energy being lost at each transfer. There is energy lost at each trophic level, so the lengths of food chains are limited because there is a point where not enough energy remains to support a population of consumers. Fat soluble compounds biomagnify up a food chain causing damage to top consumers. even when environmental concentrations of a toxin are low.

Multiple Choice

Decomposers are associated with which class of food web?

1. grazing
2. detrital
3. inverted
4. aquatic

B

The producer in an ocean grazing food web is usually a _____.

1. plant
2. animal
3. fungi
4. plankton

D

Which term describes the process whereby toxic substances increase along trophic levels of an ecosystem?

1. biomassification
2. biomagnification
3. bioentropy
4. heterotrophy

B

Free Response

Compare grazing and detrital food webs. Why would they both be present in the same ecosystem?

Grazing food webs have a producer at their base, which is either a plant for terrestrial ecosystems or a phytoplankton for aquatic ecosystems. The producers pass their energy to the various trophic levels of consumers. At the base of detrital food webs are the decomposers, which pass their energy to a variety of other consumers. Detrital food webs are important for the health of many grazing food webs because they eliminate dead and decaying organic material, thus clearing space for new organisms and removing potential causes of disease.

Glossary

autotroph
: an organism capable of synthesizing its own food molecules from smaller inorganic molecules

apex consumer
: an organism at the top of the food chain

biomagnification
: an increasing concentration of persistent, toxic substances in organisms at each trophic level, from the producers to the apex consumers

biome
: a large-scale community of organisms, primarily defined on land by the dominant plant types that exist in geographic regions of the planet with similar climatic conditions

chemoautotroph
: an organism capable of synthesizing its own food using energy from inorganic molecules

detrital food web
: a type of food web that is supported by dead or decaying organisms rather than by living autotrophs; these are often associated with grazing food webs within the same ecosystem

ecosystem
: a community of living organisms and their interactions with their abiotic environment

equilibrium
: the steady state of a system in which the relationships between elements of the system

do not change

food chain
: a linear sequence of trophic (feeding) relationships of producers, primary consumers, and higher level consumers

food web
: a web of trophic (feeding) relationships among producers, primary consumers, and higher level consumers in an ecosystem

grazing food web
: a type of food web in which the producers are either plants on land or phytoplankton in the water; often associated with a detrital food web within the same ecosystem

gross primary productivity
: the rate at which photosynthetic producers incorporate energy from the Sun

net primary productivity
: the energy that remains in the producers after accounting for the organisms’ respiration and heat loss

photoautotroph
: an organism that uses sunlight as an energy source to synthesize its own food molecules

primary consumer

the trophic level that obtains its energy from the producers of an ecosystem

producer
: the trophic level that obtains its energy from sunlight, inorganic chemicals, or dead or decaying organic material

resilience (ecological)
: the speed at which an ecosystem recovers equilibrium after being disturbed

resistance (ecological)
: the ability of an ecosystem to remain at equilibrium in spite of disturbances

secondary consumer
: a trophic level in an ecosystem, usually a carnivore that eats a primary consumer

tertiary consumer
: a trophic level in an ecosystem, usually carnivores that eat other carnivores

trophic level
: the position of a species or group of species in a food chain or a food web

Biogeochemical Cycles

By the end of this section, you will be able to do the following:

- Discuss the biogeochemical cycles of water, carbon, nitrogen, phosphorus, and sulfur
- Explain how human activities have impacted these cycles and the potential consequences for Earth

Energy flows directionally through ecosystems, entering as sunlight (or inorganic molecules for chemoautotrophs) and leaving as heat during the many transfers between trophic levels. However, the matter that makes up living organisms is conserved and recycled. The six most common elements associated with organic molecules—carbon, nitrogen, hydrogen, oxygen, phosphorus, and sulfur—take a variety of chemical forms and may exist for long periods in the atmosphere, on land, in water, or beneath the Earth's surface. Geologic processes, such as weathering, erosion, water drainage, and the subduction of the continental plates, all play a role in this recycling of materials. Because geology and chemistry have major roles in the study of this process, the recycling of inorganic matter between living organisms and their environment is called a **biogeochemical cycle**.

Water contains hydrogen and oxygen, which is essential to all living processes. The **hydrosphere** is

the area of the Earth where water movement and storage occurs. On or beneath the surface, water occurs in liquid or solid form in rivers, lakes, oceans, groundwater, polar ice caps, and glaciers. And it occurs as water vapor in the atmosphere. Carbon is found in all organic macromolecules and is an important constituent of fossil fuels. Nitrogen is a major component of our nucleic acids and proteins and is critical to human agriculture. Phosphorus, a major component of nucleic acid (along with nitrogen), is one of the main ingredients in artificial fertilizers used in agriculture and their associated environmental impacts on our surface water. Sulfur is critical to the 3-D folding of proteins, such as in disulfide binding.

The cycling of these elements is interconnected. For example, the movement of water is critical for the leaching of nitrogen and phosphate into rivers, lakes, and oceans. Furthermore, the ocean itself is a major reservoir for carbon. Thus, mineral nutrients are cycled, either rapidly or slowly, through the entire biosphere, from one living organism to another, and between the biotic and abiotic world.

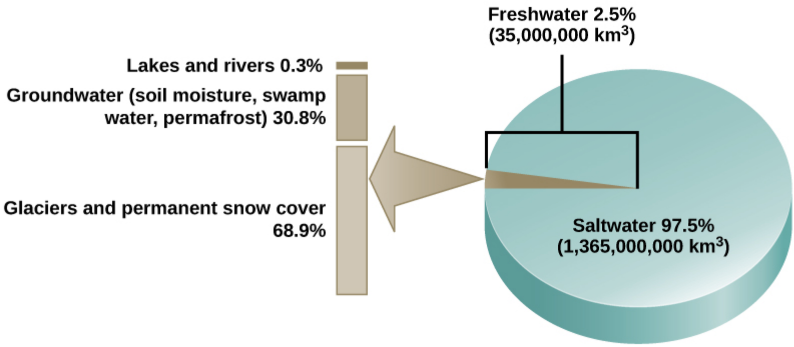
Link to Learning

Head to this website to learn more about biogeochemical cycles.

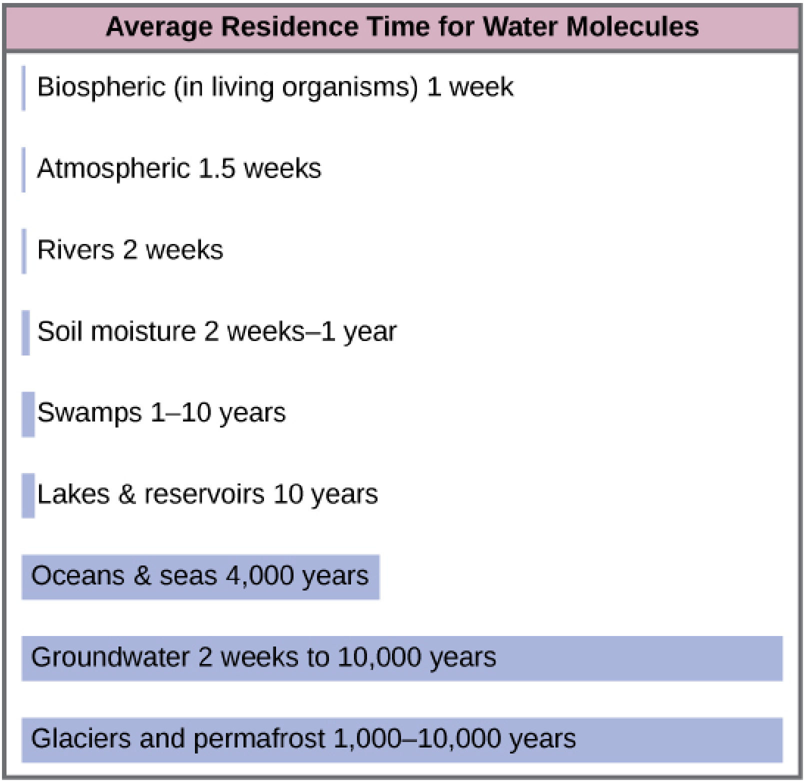
Only 2.5 percent of water on Earth is fresh water, and less than 1 percent of fresh water is easily accessible to living things. This graph shows the average residence time for water molecules in the Earth's water reservoirs. Water from the land and oceans enters the atmosphere by evaporation or sublimation, where it condenses into clouds and falls as rain or snow. Precipitated water may enter freshwater bodies or infiltrate the soil. The cycle is complete when surface or groundwater reenters the ocean. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

The Water (Hydrologic) Cycle

Water is the basis of all living processes on Earth. When examining the stores of water on Earth, 97.5 percent of it is non-potable salt water ([link]). Of the remaining water, 99 percent is locked underground as water or as ice. Thus, less than 1 percent of fresh water is easily accessible from lakes and rivers. Many living things, such as plants, animals, and fungi, are dependent on that small amount of fresh surface water, a lack of which can have massive effects on ecosystem dynamics. To be successful, organisms must adapt to fluctuating water supplies. Humans, of course, have developed technologies to increase water availability, such as digging wells to harvest groundwater, storing rainwater, and using desalination to obtain drinkable water from the ocean.



Water cycling is extremely important to ecosystem dynamics. Water has a major influence on climate and, thus, on the environments of ecosystems. Most of the water on Earth is stored for long periods in the oceans, underground, and as ice. [link] illustrates the average time that an individual water molecule may spend in the Earth’s major water reservoirs. **Residence time** is a measure of the average time an individual water molecule stays in a particular reservoir.



There are various processes that occur during the cycling of water, shown in [link]. These processes include the following:

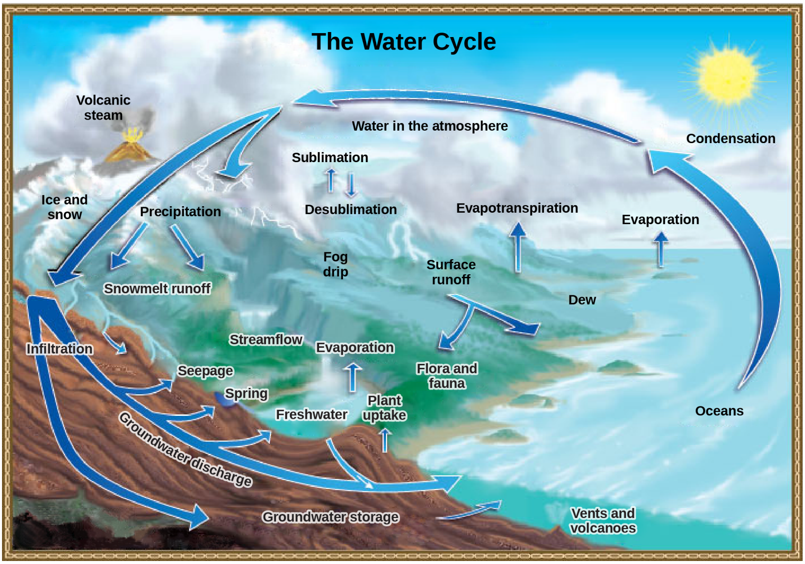
- evaporation/sublimation
- condensation/precipitation
- subsurface water flow
- surface runoff/snowmelt
- streamflow

The water cycle is driven by the sun's energy as it warms the oceans and other surface waters. This leads to the evaporation (water to water vapor) of

liquid surface water and the sublimation (ice to water vapor) of frozen water, which deposits large amounts of water vapor into the atmosphere. Over time, this water vapor condenses into clouds as liquid or frozen droplets and is eventually followed by precipitation (rain or snow), which returns water to the Earth's surface. Rain eventually permeates into the ground, where it may evaporate again if it is near the surface, flow beneath the surface, or be stored for long periods. More easily observed is surface runoff: the flow of fresh water either from rain or melting ice. Runoff can then make its way through streams and lakes to the oceans or flow directly to the oceans themselves.

> Link to Learning
> Head to this website to learn more about the world's fresh water supply.

Rain and surface runoff are major ways in which minerals, including carbon, nitrogen, phosphorus, and sulfur, are cycled from land to water. The environmental effects of runoff will be discussed later as these cycles are described.



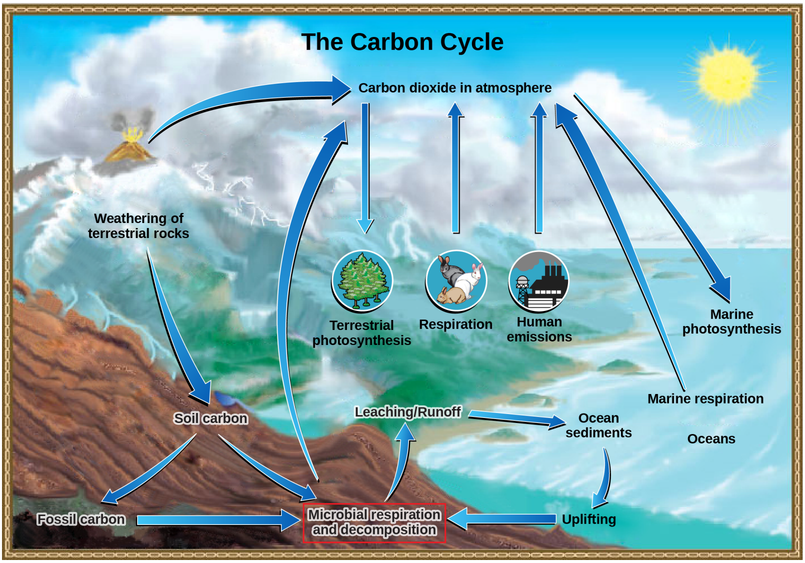
Carbon dioxide gas exists in the atmosphere and is dissolved in water. Photosynthesis converts carbon dioxide gas to organic carbon, and respiration cycles the organic carbon back into carbon dioxide gas. Long-term storage of organic carbon occurs when matter from living organisms is buried deep underground and becomes fossilized. Volcanic activity and, more recently, human emissions, bring this stored carbon back into the carbon cycle. (credit: modification of work by John M. Evans and Howard Perlman, USGS) Carbon dioxide reacts with water to form bicarbonate and carbonate ions.

The Carbon Cycle

Carbon is the second most abundant element in living organisms. Carbon is present in all organic molecules, and its role in the structure of

macromolecules is of primary importance to living organisms.

The carbon cycle is most easily studied as two interconnected sub-cycles: one dealing with rapid carbon exchange among living organisms and the other dealing with the long-term cycling of carbon through geologic processes. The entire carbon cycle is shown in [link].



Link to Learning
Click this link to read information about the United States Carbon Cycle Science Program.

The Biological Carbon Cycle

Living organisms are connected in many ways, even between ecosystems. A good example of this connection is the exchange of carbon between autotrophs and heterotrophs within and between ecosystems by way of atmospheric carbon dioxide. Carbon dioxide is the basic building block that most autotrophs use to build multicarbon, high energy compounds, such as glucose. The energy harnessed from the sun is used by these organisms to form the covalent bonds that link carbon atoms together. These chemical bonds thereby store this energy for later use in the process of respiration. Most terrestrial autotrophs obtain their carbon dioxide directly from the atmosphere, while marine autotrophs acquire it in the dissolved form (carbonic acid, $H_2CO_3^-$). However carbon dioxide is acquired, a by-product of the process is oxygen. The photosynthetic organisms are responsible for depositing approximately 21 percent oxygen content of the atmosphere that we observe today.

Heterotrophs and autotrophs are partners in biological carbon exchange (especially the primary consumers, largely herbivores). Heterotrophs acquire the high-energy carbon compounds from the autotrophs by consuming them, and breaking them down by respiration to obtain cellular energy, such as ATP. The most efficient type of respiration, aerobic respiration, requires oxygen obtained from the atmosphere or dissolved in water. Thus, there is a constant exchange of oxygen and carbon dioxide

between the autotrophs (which need the carbon) and the heterotrophs (which need the oxygen). Gas exchange through the atmosphere and water is one way that the carbon cycle connects all living organisms on Earth.

The Biogeochemical Carbon Cycle

The movement of carbon through the land, water, and air is complex, and in many cases, it occurs much more slowly geologically than as seen between living organisms. Carbon is stored for long periods in what are known as carbon reservoirs, which include the atmosphere, bodies of liquid water (mostly oceans), ocean sediment, soil, land sediments (including fossil fuels), and the Earth's interior.

As stated, the atmosphere is a major reservoir of carbon in the form of carbon dioxide and is essential to the process of photosynthesis. The level of carbon dioxide in the atmosphere is greatly influenced by the reservoir of carbon in the oceans. The exchange of carbon between the atmosphere and water reservoirs influences how much carbon is found in each location, and each one affects the other reciprocally. Carbon dioxide (CO_2) from the atmosphere dissolves in water and combines with water molecules to form carbonic acid, and then it ionizes to carbonate and bicarbonate ions ([link])

Step 1: CO_2 (atmospheric) $\rightleftharpoons$ CO_2 (dissolved)
Step 2: CO_2 (dissolved) + $H_2O \rightleftharpoons H_2CO_3$ (carbonic acid)
Step 3: $H_2CO_3 \rightleftharpoons + H^+ + HCO_3^-$ (biocarbonate ion)
Step 4: $HCO_3^- \rightleftharpoons H^+ + CO_3^{2-}$ (carbonate ion)

The equilibrium coefficients are such that more than 90 percent of the carbon in the ocean is found as bicarbonate ions. Some of these ions combine with seawater calcium to form calcium carbonate ($CaCO_3$), a major component of marine organism shells. These organisms eventually form sediments on the ocean floor. Over geologic time, the calcium carbonate forms limestone, which comprises the largest carbon reservoir on Earth.

On land, carbon is stored in soil as a result of the decomposition of living organisms (by decomposers) or from weathering of terrestrial rock and minerals. This carbon can be leached into the water reservoirs by surface runoff. Deeper underground, on land and at sea, are fossil fuels: the anaerobically decomposed remains of plants that take millions of years to form. Fossil fuels are considered a nonrenewable resource because their use far exceeds their rate of formation. A **nonrenewable resource**, such as fossil fuel, is either regenerated very slowly or not at all. Another way for carbon to enter the atmosphere is from land (including land beneath the surface of the ocean) by the eruption of volcanoes

and other geothermal systems. Carbon sediments from the ocean floor are taken deep within the Earth by the process of **subduction**: the movement of one tectonic plate beneath another. Carbon is released as carbon dioxide when a volcano erupts or from volcanic hydrothermal vents.

Humans contribute to atmospheric carbon by the burning of fossil fuels and other materials. Since the Industrial Revolution, humans have significantly increased the release of carbon and carbon compounds, which has in turn affected the climate and overall environment.

Animal husbandry by humans also increases atmospheric carbon. The large numbers of land animals raised to feed the Earth's growing population results in increased carbon dioxide levels in the atmosphere due to farming practices and respiration and methane production. This is another example of how human activity indirectly affects biogeochemical cycles in a significant way. Although much of the debate about the future effects of increasing atmospheric carbon on climate change focuses on fossils fuels, scientists take natural processes, such as volcanoes and respiration, into account as they model and predict the future impact of this increase.

Scott L. Morford, Benjamin Z. Houlton, and Randy A. Dahlgren, "Increased Forest Ecosystem Carbon and Nitrogen Storage from Nitrogen Rich Bedrock,"

Nature 477, no. 7362 (2011): 78–81.

The Nitrogen Cycle

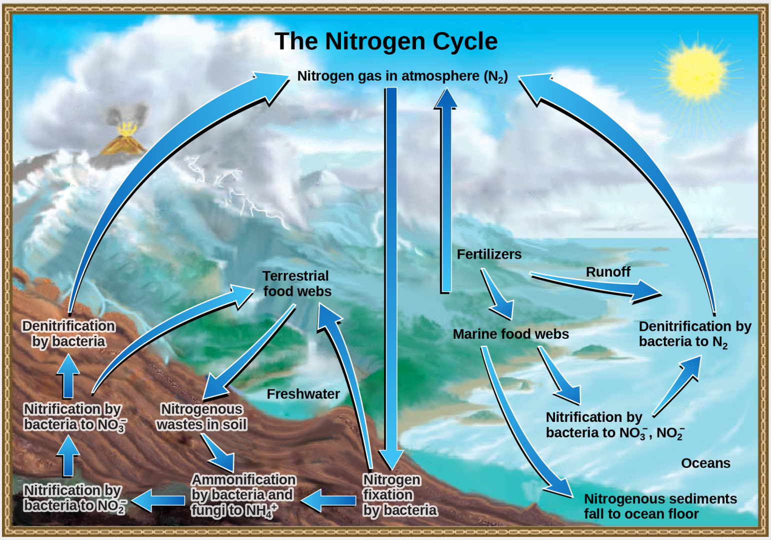
Getting nitrogen into the living world is difficult. Plants and phytoplankton are not equipped to incorporate nitrogen from the atmosphere (which exists as tightly bonded, triple covalent N_2) even though this molecule comprises approximately 78 percent of the atmosphere. Nitrogen enters the living world via free-living and symbiotic bacteria, which incorporate nitrogen into their macromolecules through nitrogen fixation (conversion of N_2). Cyanobacteria live in most aquatic ecosystems where sunlight is present; they play a key role in nitrogen fixation. Cyanobacteria are able to use inorganic sources of nitrogen to "fix" nitrogen. *Rhizobium* bacteria live symbiotically in the root nodules of legumes (such as peas, beans, and peanuts) and provide them with the organic nitrogen they need. (For example, gardeners often grow peas both for their produce and to naturally add nitrogen to the soil. This practice goes back to ancient times, even if the science has only been recently understood.) Free-living bacteria, such as *Azotobacter*, are also important nitrogen fixers.

Organic nitrogen is especially important to the study of ecosystem dynamics since many ecosystem processes, such as primary production and decomposition, are limited by the available supply

of nitrogen. As shown in [link], the nitrogen that enters living systems by nitrogen fixation is successively converted from organic nitrogen back into nitrogen gas by bacteria. This process occurs in three steps in terrestrial systems: ammonification, nitrification, and denitrification. First, the ammonification process converts nitrogenous waste from living animals or from the remains of dead animals into ammonium (NH_4^+) by certain bacteria and fungi. Second, the ammonium is converted to nitrites (NO_2^-) by nitrifying bacteria, such as *Nitrosomonas*, through nitrification. Subsequently, nitrites are converted to nitrates (NO_3^-) by similar organisms. Third, the process of denitrification occurs, whereby bacteria, such as *Pseudomonas* and *Clostridium*, convert the nitrates into nitrogen gas, allowing it to reenter the atmosphere.

Visual Connection

Nitrogen enters the living world from the atmosphere via nitrogen-fixing bacteria. This nitrogen and nitrogenous waste from animals is then processed back into gaseous nitrogen by soil bacteria, which also supply terrestrial food webs with the organic nitrogen they need. (credit: modification of work by John M. Evans and Howard Perlman, USGS)



Which of the following statements about the nitrogen cycle is false?

1. Ammonification converts organic nitrogenous matter from living organisms into ammonium (NH_4^+).
2. Denitrification by bacteria converts nitrates (NO_3^-) to nitrogen gas (N_2).
3. Nitrification by bacteria converts nitrates (NO_3^-) to nitrites (NO_2^-).
4. Nitrogen fixing bacteria convert nitrogen gas (N_2) into organic compounds.

Human activity can release nitrogen into the environment by two primary means: the combustion of fossil fuels, which releases different nitrogen oxides, and by the use of artificial fertilizers in

agriculture, which are then washed into lakes, streams, and rivers by surface runoff. Atmospheric nitrogen is associated with several effects on Earth's ecosystems including the production of acid rain (as nitric acid, HNO_3) and greenhouse gas (as nitrous oxide, N_2O) potentially causing climate change. A major effect from fertilizer runoff is saltwater and freshwater **eutrophication**, a process whereby nutrient runoff causes the excess growth of microorganisms, depleting dissolved oxygen levels and killing ecosystem fauna.

A similar process occurs in the marine nitrogen cycle, where the ammonification, nitrification, and denitrification processes are performed by marine bacteria. Some of this nitrogen falls to the ocean floor as sediment, which can then be moved to land in geologic time by uplift of the Earth's surface and thereby incorporated into terrestrial rock. Although the movement of nitrogen from rock directly into living systems has been traditionally seen as insignificant compared with nitrogen fixed from the atmosphere, a recent study showed that this process may indeed be significant and should be included in any study of the global nitrogen cycle.[footnote]

In nature, phosphorus exists as the phosphate ion (PO_4^{3-}). Weathering of rocks and volcanic activity releases phosphate into the soil, water, and air, where it becomes available to terrestrial food webs. Phosphate enters the oceans via surface runoff, groundwater flow, and river flow. Phosphate

dissolved in ocean water cycles into marine food webs. Some phosphate from the marine food webs falls to the ocean floor, where it forms sediment. (credit: modification of work by John M. Evans and Howard Perlman, USGS)Dead zones occur when phosphorus and nitrogen from fertilizers cause excessive growth of microorganisms, which depletes oxygen and kills fauna. Worldwide, large dead zones are found in coastal areas of high population density. (credit: NASA Earth Observatory)

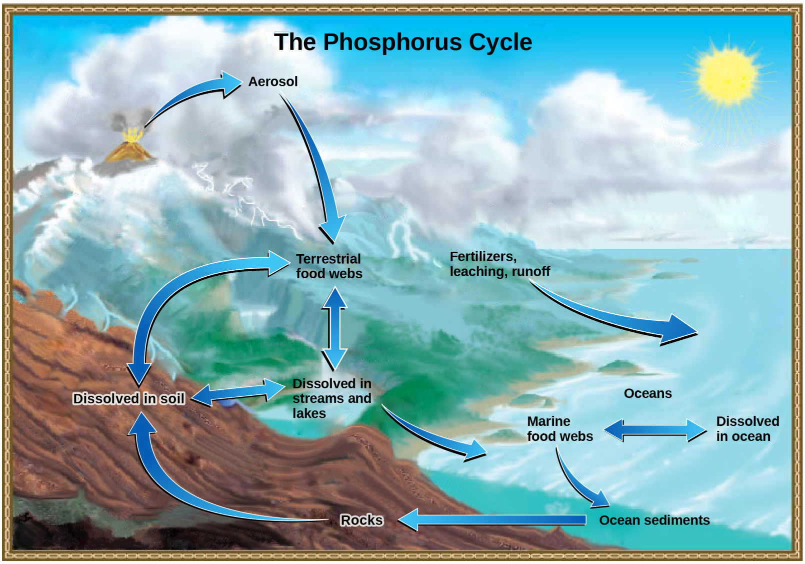
The Phosphorus Cycle

Phosphorus is an essential nutrient for living processes; it is a major component of nucleic acid and phospholipids, and, as calcium phosphate, makes up the supportive components of our bones. Phosphorus is often the limiting nutrient (necessary for growth) in aquatic ecosystems ([link]).

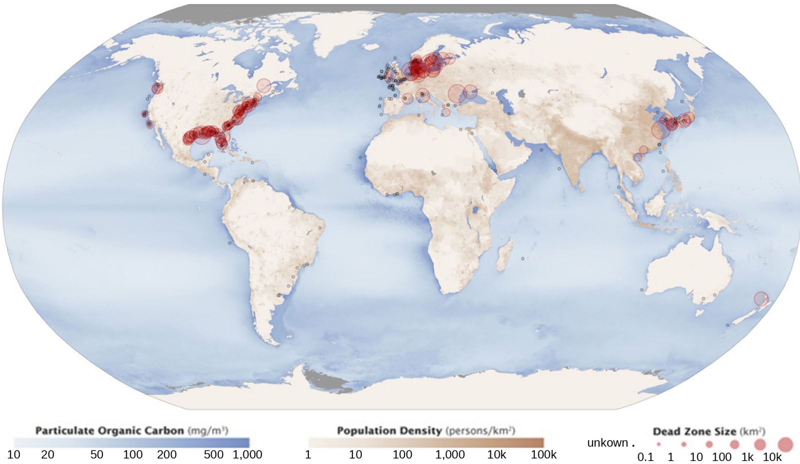
Phosphorus occurs in nature as the phosphate ion (PO_4^{3-}). In addition to phosphate runoff as a result of human activity, natural surface runoff occurs when it is leached from phosphate-containing rock by weathering, thus sending phosphates into rivers, lakes, and the ocean. This rock has its origins in the ocean. Phosphate-containing ocean sediments form primarily from the bodies of ocean organisms and from their excretions. However, in remote regions, volcanic ash, aerosols, and mineral dust may also be significant phosphate sources. This sediment then is

moved to land over geologic time by the uplifting of areas of the Earth’s surface.

Phosphorus is also reciprocally exchanged between phosphate dissolved in the ocean and marine ecosystems. The movement of phosphate from the ocean to the land and through the soil is extremely slow, with the average phosphate ion having an oceanic residence time between 20,000 and 100,000 years.



As discussed in Chapter 44, excess phosphorus and nitrogen that enters these ecosystems from fertilizer runoff and from sewage causes excessive growth of microorganisms and depletes the dissolved oxygen, which leads to the death of many ecosystem fauna, such as shellfish and finfish. This process is responsible for dead zones in lakes and at the mouths of many major rivers ([link]).

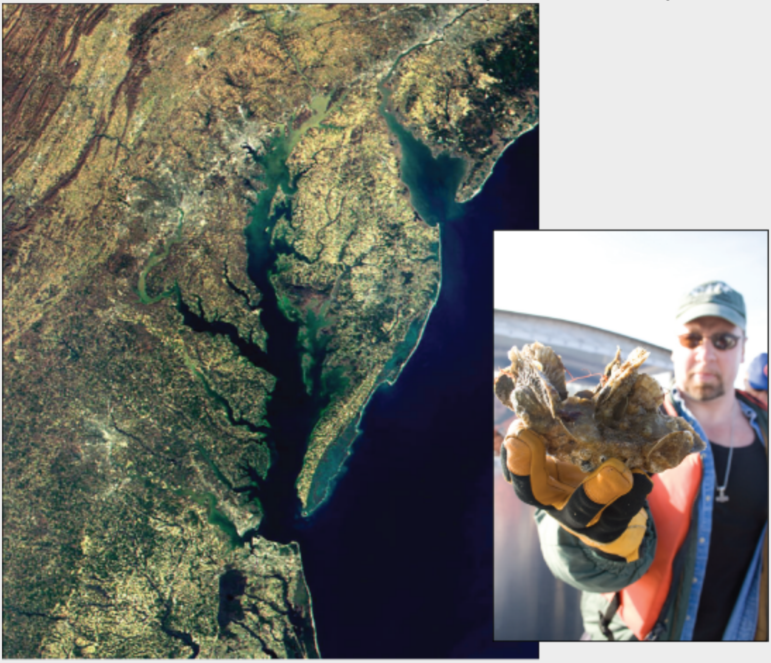


As discussed earlier, a **dead zone** is an area within a freshwater or marine ecosystem where large areas are depleted of their normal flora and fauna; these zones can be caused by eutrophication, oil spills, dumping of toxic chemicals, and other human activities. The number of dead zones has been increasing for several years, and more than 400 of these zones were present as of 2008. One of the worst dead zones is off the coast of the United States in the Gulf of Mexico, where fertilizer runoff from the Mississippi River basin has created a dead zone of over 8463 square miles. Phosphate and nitrate runoff from fertilizers also negatively affect several lake and bay ecosystems including the Chesapeake Bay in the eastern United States.

Everyday Connection

Chesapeake Bay

This (a) satellite image shows the Chesapeake Bay, an ecosystem affected by phosphate and nitrate runoff. A (b) member of the Army Corps of Engineers holds a clump of oysters being used as a part of the oyster restoration effort in the bay. (credit a: modification of work by NASA/MODIS; credit b: modification of work by U.S. Army)



(a) (b)

The Chesapeake Bay has long been valued as one of the most scenic areas on Earth; it is now in distress and is recognized as a declining ecosystem. In the 1970s, the Chesapeake Bay was one of the first ecosystems to have identified dead zones, which continue to kill many fish and bottom-dwelling species, such as clams, oysters, and worms. Several species have declined in the

Chesapeake Bay due to surface water runoff containing excess nutrients from artificial fertilizer used on land. The source of the fertilizers (with high nitrogen and phosphate content) is not limited to agricultural practices. There are many nearby urban areas and more than 150 rivers and streams empty into the bay that are carrying fertilizer runoff from lawns and gardens. Thus, the decline of the Chesapeake Bay is a complex issue and requires the cooperation of industry, agriculture, and everyday homeowners.

Of particular interest to conservationists is the oyster population; it is estimated that more than 200,000 acres of oyster reefs existed in the bay in the 1700s, but that number has now declined to only 36,000 acres. Oyster harvesting was once a major industry for Chesapeake Bay, but it declined 88 percent between 1982 and 2007. This decline was due not only to fertilizer runoff and dead zones but also to overharvesting. Oysters require a certain minimum population density because they must be in close proximity to reproduce. Human activity has altered the oyster population and locations, greatly disrupting the ecosystem.

The restoration of the oyster population in the Chesapeake Bay has been ongoing for several years with mixed success. Not only do many people find oysters good to eat, but they also clean up the bay. Oysters are filter feeders, and as they eat, they clean the water around them. In the 1700s, it was estimated that it took only a few days for the

oyster population to filter the entire volume of the bay. Today, with changed water conditions, it is estimated that the present population would take nearly a year to do the same job.

Restoration efforts have been ongoing for several years by nonprofit organizations, such as the Chesapeake Bay Foundation. The restoration goal is to find a way to increase population density so the oysters can reproduce more efficiently. Many disease-resistant varieties (developed at the Virginia Institute of Marine Science for the College of William and Mary) are now available and have been used in the construction of experimental oyster reefs. Efforts to clean and restore the bay by Virginia and Delaware have been hampered because much of the pollution entering the bay comes from other states, which stresses the need for interstate cooperation to gain successful restoration.

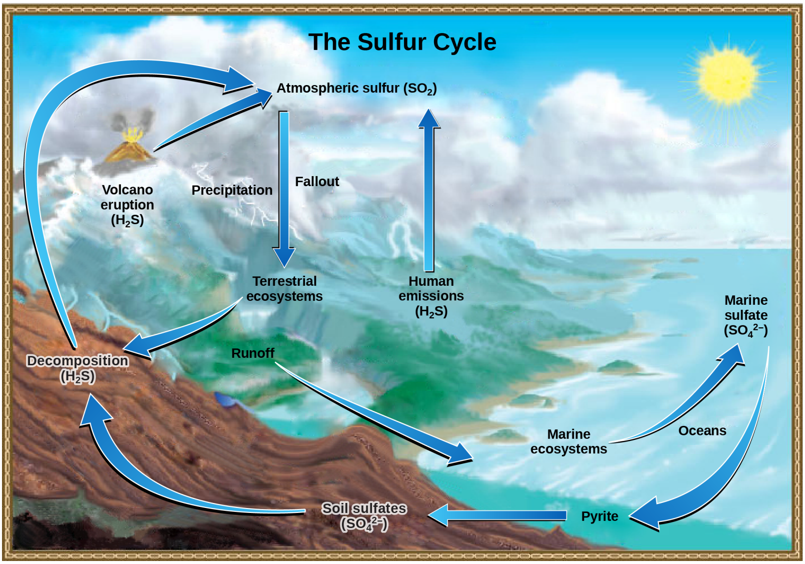
The new, hearty oyster strains have also spawned a new and economically viable industry—oyster aquaculture—which not only supplies oysters for food and profit, but also has the added benefit of cleaning the bay.

Sulfur dioxide from the atmosphere becomes available to terrestrial and marine ecosystems when it is dissolved in precipitation as weak sulfuric acid or when it falls directly to the Earth as fallout.

Weathering of rocks also makes sulfates available to terrestrial ecosystems. Decomposition of living organisms returns sulfates to the ocean, soil, and atmosphere. (credit: modification of work by John M. Evans and Howard Perlman, USGS) At this sulfur vent in Lassen Volcanic National Park in northeastern California, the yellowish sulfur deposits are visible near the mouth of the vent.

The Sulfur Cycle

Sulfur is an essential element for the macromolecules of living things. As a part of the amino acid cysteine, it is involved in the formation of disulfide bonds within proteins, which help to determine their 3-D folding patterns, and hence their functions. As shown in [link], sulfur cycles between the oceans, land, and atmosphere. Atmospheric sulfur is found in the form of sulfur dioxide (SO_2) and enters the atmosphere in three ways: from the decomposition of organic molecules, from volcanic activity and geothermal vents, and from the burning of fossil fuels by humans.



On land, sulfur is deposited in four major ways: precipitation, direct fallout from the atmosphere, rock weathering, and geothermal vents ([link]). Atmospheric sulfur is found in the form of sulfur dioxide (SO_2), and as rain falls through the atmosphere, sulfur is dissolved in the form of weak sulfuric acid (H_2SO_4). Sulfur can also fall directly from the atmosphere in a process called **fallout**. Also, the weathering of sulfur-containing rocks releases sulfur into the soil. These rocks originate from ocean sediments that are moved to land by the geologic uplifting of ocean sediments. Terrestrial ecosystems can then make use of these soil sulfates (SO_4^{-}), and upon the death and decomposition of these organisms, release the sulfur back into the atmosphere as hydrogen sulfide (H_2S) gas.

Sulfur enters the ocean via runoff from land, from atmospheric fallout, and from underwater geothermal vents. Some ecosystems ([link]) rely on chemoautotrophs using sulfur as a biological energy source. This sulfur then supports marine ecosystems in the form of sulfates.

Human activities have played a major role in altering the balance of the global sulfur cycle. The burning of large quantities of fossil fuels, especially from coal, releases larger amounts of hydrogen sulfide gas into the atmosphere. **Acid rain** is caused by rainwater falling to the ground through this sulfur dioxide gas, turning it into weak sulfuric acid. Acid rain damages the natural environment by lowering the pH of lakes, which kills many of the resident fauna; it also affects the man-made

environment through the chemical degradation of buildings. For example, many marble monuments, such as the Lincoln Memorial in Washington, DC, have suffered significant damage from acid rain over the years.

Link to Learning
Click this link to learn more about global climate change.

Section Summary

Mineral nutrients are cycled through ecosystems and their environment. Of particular importance are water, carbon, nitrogen, phosphorus, and sulfur. All of these cycles have major impacts on ecosystem structure and function. A variety of human activities, such as pollution, oil spills, and other events have damaged ecosystems, potentially causing global climate change. The health of Earth depends on understanding these cycles and how to protect the environment from irreversible damage.

Visual Connection Questions

[link] Which of the following statements about the nitrogen cycle is false?

1. Ammonification converts organic nitrogenous matter from living organisms into ammonium (NH_4^+).
2. Denitrification by bacteria converts nitrates (NO_3^-) to nitrogen gas (N_2).
3. Nitrification by bacteria converts nitrates (NO_3^-) to nitrites (NO_2^-).
4. Nitrogen fixing bacteria convert nitrogen gas (N_2) into organic compounds.

[link] C: Nitrification by bacteria converts nitrates (NO_3^-) to nitrites (NO_2^-).

Review Questions

The movement of mineral nutrients through organisms and their environment is called a ______ cycle.

1. biological
2. bioaccumulation

3. biogeochemical
4. biochemical

C

Carbon is present in the atmosphere as ______.

1. carbon dioxide
2. carbonate ion
3. carbon dust
4. carbon monoxide

A

The majority of water found on Earth is:

1. ice
2. water vapor
3. fresh water
4. salt water

D

The average time a molecule spends in its reservoir is known as ______.

1. residence time
2. restriction time
3. resilience time
4. storage time

A

The process whereby oxygen is depleted by the growth of microorganisms due to excess nutrients in aquatic systems is called ______.

1. dead zoning
2. eutrophication
3. retrofication
4. depletion

B

The process whereby nitrogen is brought into organic molecules is called ______.

1. nitrification
2. denitrification
3. nitrogen fixation
4. nitrogen cycling

C

Which of the following approaches would be the most effective way to reduce greenhouse carbon dioxide?

1. Increase waste deposition into the deep ocean.
2. Plant more environmentally-suitable plants.
3. Increase use of fuel sources that do not produce carbon dioxide as a by-product.
4. Decrease livestock agriculture.

B

How would loss of fungi in a forest effect biogeochemical cycles in the area?

1. Nitrogen could no longer be fixed into organic molecules.
2. Phosphorus stores would be released for use by other organisms.
3. Sulfur release from eroding rocks would cease.
4. Carbon would accumulate in dead organic matter and waste.

D

Critical Thinking Questions

Describe nitrogen fixation and why it is important to agriculture.

Nitrogen fixation is the process of bringing nitrogen gas from the atmosphere and incorporating it into organic molecules. Most plants do not have this capability and must rely on free-living or symbiotic bacteria to do this. As nitrogen is often the limiting nutrient in the growth of crops, farmers make use of artificial fertilizers to provide a nitrogen source to the plants as they grow.

What are the factors that cause dead zones? Describe eutrophication, in particular, as a cause.

Many factors can kill life in a lake or ocean, such as eutrophication by nutrient-rich surface runoff, oil spills, toxic waste spills, changes in climate, and the dumping of garbage into the ocean. Eutrophication is a result of nutrient-rich runoff from land using artificial fertilizers high in nitrogen and phosphorus. These nutrients cause the rapid and excessive growth of

microorganisms, which deplete local dissolved oxygen and kill many fish and other aquatic organisms.

Why are drinking water supplies still a major concern for many countries?

Most of the water on Earth is salt water, which humans cannot drink unless the salt is removed. Some fresh water is locked in glaciers and polar ice caps, or is present in the atmosphere. The Earth's water supplies are threatened by pollution and exhaustion. The effort to supply fresh drinking water to the planet's ever-expanding human population is seen as a major challenge in this century.

Discuss how the human disruption of the carbon cycle has caused ocean acidification.

Human activity has greatly increased the amount of carbon dioxide gas in the Earth's atmosphere. The oceanic and atmospheric levels of carbon dioxide are linked so that when atmospheric carbon dioxide levels increase, the amount of dissolved carbon dioxide in the ocean also increases (partial pressure of oxygen). When carbon dioxide dissolves in

water it produces the weak acid bicarbonate. Since the Industrial Revolution the pH of the ocean has dropped 0.1 pH units, a 30% increase in acidity.

Glossary

acid rain
: corrosive rain caused by rainwater falling to the ground through sulfur dioxide gas, turning it into weak sulfuric acid; can damage structures and ecosystems

biogeochemical cycle
: cycling of mineral nutrients through ecosystems and through the nonliving world

dead zone
: area within an ecosystem in lakes and near the mouths of rivers where large areas of ecosystems are depleted of their normal flora and fauna; these zones can be caused by eutrophication, oil spills, dumping of toxic chemicals, and other human activities

eutrophication
: process whereby nutrient runoff causes the excess growth of microorganisms, depleting dissolved oxygen levels and killing ecosystem fauna

fallout
: direct deposit of solid minerals on land or in the ocean from the atmosphere

hydrosphere
: area of the Earth where water movement and storage occurs

nonrenewable resource
: resource, such as fossil fuel, that is either regenerated very slowly or not at all

residence time
: measure of the average time an individual water molecule stays in a particular reservoir

subduction
: movement of one tectonic plate beneath another

Terrestrial Biomes

By the end of this section, you will be able to do the following:

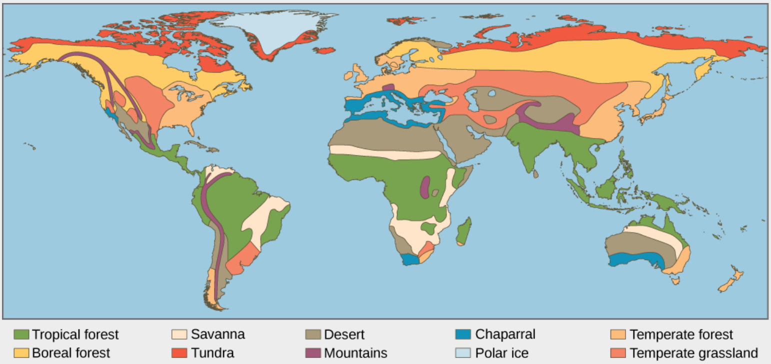
- Identify the two major abiotic factors that determine terrestrial biomes
- Recognize distinguishing characteristics of each of the eight major terrestrial biomes

The Earth’s biomes are categorized into two major groups: *terrestrial* and *aquatic*. **Terrestrial biomes** are based on land, while **aquatic biomes** include both ocean and freshwater biomes. The eight major terrestrial biomes on Earth are each distinguished by characteristic temperatures and amount of precipitation. Comparing the annual totals of precipitation and fluctuations in precipitation from one biome to another provides clues as to the importance of abiotic factors in the distribution of biomes. Temperature variation on a daily and seasonal basis is also important for predicting the geographic distribution of the biome and the vegetation type in the biome. The distribution of these biomes shows that the same biome can occur in geographically distinct areas with similar climates ([link]).

Visual Connection

Each of the world’s major biomes is distinguished

by characteristic temperatures and amounts of precipitation. Polar ice and mountains are also shown.



Which of the following statements about biomes is false?

1. Chaparral is dominated by shrubs.
2. Savannas and temperate grasslands are dominated by grasses.
3. Boreal forests are dominated by deciduous trees.
4. Lichens are common in the arctic tundra.

Tropical wet forests, such as these forests along the Madre de Dios river, Peru, near the Amazon River, have high species diversity. (credit: Roosevelt Garcia)

Tropical Wet Forest

Tropical wet forests are also referred to as tropical

rainforests. This biome is found in equatorial regions ([link]). The vegetation is characterized by plants with broad leaves that fall and are replaced throughout the year. Unlike the trees of deciduous forests, the trees in this biome do not have a seasonal loss of leaves associated with variations in temperature and sunlight; these forests are "evergreen" year-round.

The temperature and sunlight profiles of tropical wet forests are very stable in comparison to that of other terrestrial biomes, with the temperatures ranging from 20 °C to 34 °C (68 °F to 93 °F). When one compares the annual temperature variation of tropical wet forests with that of other forest biomes, the lack of seasonal temperature variation in the tropical wet forest becomes apparent. This lack of seasonality leads to year-round plant growth, rather than the seasonal (spring, summer, and fall) growth seen in other more temperate biomes. In contrast to other ecosystems, tropical ecosystems do not have long days and short days during the yearly cycle. Instead, a constant daily amount of sunlight (11–12 hrs per day) provides more solar radiation, thereby, a longer period of time for plant growth.

The annual rainfall in tropical wet forests ranges from 125 cm to 660 cm (50–200 in) with some monthly variation. While sunlight and temperature remain fairly consistent, annual rainfall is highly variable. Tropical wet forests typically have wet

months in which there can be more than 30 cm (11–12 in) of precipitation, as well as dry months in which there are fewer than 10 cm (3.5 in) of rainfall. However, the driest month of a tropical wet forest still exceeds the *annual* rainfall of some other biomes, such as deserts.

Tropical wet forests have high net primary productivity because the annual temperatures and precipitation values in these areas are ideal for plant growth. Therefore, the extensive biomass present in the tropical wet forest leads to plant communities with very high species diversities ([link]). Tropical wet forests have more species of trees than any other biome; on average between 100 and 300 species of trees are present in a single hectare (2.5 acres) of South American Amazonian rain forest. One way to visualize this is to compare the distinctive horizontal layers within the tropical wet forest biome. On the forest floor is a sparse layer of plants and decaying plant matter. Above that is an understory of short shrubby foliage. A layer of trees rises above this understory and is topped by a closed upper **canopy**—the uppermost overhead layer of branches and leaves. Some additional trees emerge through this closed upper canopy. These layers provide diverse and complex habitats for the variety of plants, fungi, animals, and other organisms within the tropical wet forests.

For example, **epiphytes** are plants that grow on

other plants, which typically are not harmed. Epiphytes are found throughout tropical wet forest biomes. Many species of animals use the variety of plants and the complex structure of the tropical wet forests for food and shelter. Some organisms live several meters above ground and have adapted to this arboreal lifestyle.

Savannas, like this one in Taita Hills Wildlife Sanctuary in Kenya, are dominated by grasses. (credit: Christopher T. Cooper)

Savannas

Savannas are grasslands with scattered trees, and they are located in Africa, South America, and northern Australia ([link]). Savannas are usually hot, tropical areas with temperatures averaging

from 24 °C to 29 °C (75 °F to 84 °F) and an annual rainfall of 10–40 cm (3.9–15.7 in). Savannas have an extensive dry season; for this reason, forest trees do not grow as well as they do in the tropical wet forest (or other forest biomes). As a result, within the grasses and *forbs* (herbaceous flowering plants) that dominate the savanna, there are relatively few trees ([link]). Since fire is an important source of disturbance in this biome, plants have evolved well-developed root systems that allow them to quickly resprout after a fire.

To reduce water loss, many desert plants have tiny leaves or no leaves at all. The leaves of ocotillo (*Fouquieria splendens*), shown here in the Sonora Desert near Gila Bend, Arizona, appear only after rainfall, and then are shed.

Subtropical Deserts

Subtropical deserts exist between 15° and 30° north and south latitude and are centered on the Tropics of Cancer and Capricorn ([link]). This biome is very dry; in some years, evaporation exceeds precipitation. Subtropical hot deserts can have daytime soil surface temperatures above 60 °C (140 °F) and nighttime temperatures approaching 0 °C (32 °F). This is largely due to the lack of atmospheric water. In cold deserts, temperatures can be as high as 25 °C and can drop below -30 °C (-22 °F). Subtropical deserts are characterized by low annual precipitation of fewer than 30 cm (12 in) with little monthly variation and lack of predictability in rainfall. In some cases, the annual rainfall can be as low as 2 cm (0.8 in) in subtropical deserts located in central Australia ("the Outback") and northern Africa.

The vegetation and low animal diversity of this biome is closely related to low and unpredictable precipitation. Very dry deserts lack perennial vegetation that lives from one year to the next; instead, many plants are annuals that grow quickly and reproduce when rainfall does occur, and then die. Many other plants in these areas are characterized by having a number of adaptations that conserve water, such as deep roots, reduced foliage, and water-storing stems ([link]). Seed plants in the desert produce seeds that can be in dormancy for extended periods between rains. Adaptations in desert animals include nocturnal behavior and

burrowing.

The chaparral is dominated by shrubs. (credit: Miguel Vieira)

Chaparral

The chaparral is also called the scrub forest and is found in California, along the Mediterranean Sea,

and along the southern coast of Australia ([link]). The annual rainfall in this biome ranges from 65 cm to 75 cm (25.6–29.5 in), and the majority of the rain falls in the winter. Summers are very dry and many chaparral plants are dormant during the summertime. The chaparral vegetation, shown in [link], is dominated by shrubs adapted to periodic fires, with some plants producing seeds that only germinate after a hot fire. The ashes left behind after a fire are rich in nutrients like nitrogen that fertilize the soil and promote plant regrowth.

The American bison (*Bison bison*), more commonly called the buffalo, is a grazing mammal that once populated American prairies in huge numbers. (credit: Jack Dykinga, USDA Agricultural Research Service)

Temperate Grasslands

Temperate grasslands are found throughout central North America, where they are also known as *prairies*; they are also in Eurasia, where they are known as *steppes* ([link]). Temperate grasslands have pronounced annual fluctuations in temperature with hot summers and cold winters. The annual temperature variation produces specific growing seasons for plants. Plant growth is possible when temperatures are warm enough to sustain plant growth and when ample water is available, which occurs in the spring, summer, and fall. During much of the winter, temperatures are low, and water, which is stored in the form of ice, is not available for plant growth.

Annual precipitation ranges from 25 cm to 75 cm (9.8–29.5 in). Because of relatively lower annual precipitation in temperate grasslands, there are few trees except for those found growing along rivers or streams. The dominant vegetation tends to consist of grasses dense enough to sustain populations of grazing animals [link]. The vegetation is very dense and the soils are fertile because the subsurface of the soil is packed with the roots and *rhizomes* (underground stems) of these grasses. The roots and rhizomes act to anchor plants into the ground and replenish the organic material (humus) in the soil when they die and decay.

Fires, mainly caused by lightning, are a *natural disturbance* in temperate grasslands. When fire is suppressed in temperate grasslands, the vegetation eventually converts to scrub and sometimes dense forests with drought-tolerant tree species. Often, the restoration or management of temperate grasslands requires the use of controlled burns to suppress the growth of trees and maintain the grasses.
Deciduous trees are the dominant plant in the temperate forest. (credit: Oliver Herold)

Temperate Forests

Temperate forests are the most common biome in eastern North America, Western Europe, Eastern Asia, Chile, and New Zealand ([link]). This biome is found throughout mid-latitude regions. Temperatures range between -30 °C and 30 °C (-22

°F to 86 °F) and drop to below freezing periodically during cold winters. These temperatures mean that temperate forests have defined growing seasons during the spring, summer, and early fall. Precipitation is relatively constant throughout the year and ranges between 75 cm and 150 cm (29.5–59 in).

Because of the moderate annual rainfall and temperatures, deciduous trees are the dominant plant in this biome ([link]). Deciduous trees lose their leaves each fall and remain leafless in the winter. Thus, no photosynthesis occurs in the deciduous trees during the dormant winter period. Each spring, new leaves appear as the temperature increases. Because of the dormant period, the net primary productivity of temperate forests is less than that of tropical wet forests. In addition, temperate forests show less diversity of tree species than tropical wet forest biomes.

The trees of the temperate forests leaf out and shade much of the ground; however, this biome is more open than tropical wet forests because most trees in the temperate forests do not grow as tall as the trees in tropical wet forests. The soils of the temperate forests are rich in inorganic and organic nutrients. This is due to the thick layer of leaf litter on forest floors, which does not develop in tropical rainforests. As this leaf litter decays, nutrients are returned to the soil. The leaf litter also protects soil from erosion, insulates the ground, and provides habitats for invertebrates (such as the pill bug or roly-poly, *Armadillidium vulgare*) and their predators, such as the red-backed salamander (*Plethodon cinereus*).

The boreal forest (taiga) has low lying plants and conifer trees. (credit: L.B. Brubaker)

Boreal Forests

The **boreal forest**, also known as **taiga** or coniferous forest, is found south of the Arctic Circle and across most of Canada, Alaska, Russia, and northern Europe ([link]). This biome has cold, dry winters and short, cool, wet summers. The annual precipitation is from 40 cm to 100 cm (15.7–39 in) and usually takes the form of snow. Little evaporation occurs because of the cold temperatures.

The long and cold winters in the boreal forest have led to the predominance of cold-tolerant cone-bearing (coniferous) plants. These are evergreen coniferous trees like pines, spruce, and fir, which retain their needle-shaped leaves year-round. Evergreen trees can photosynthesize earlier in the spring than deciduous trees because less energy from the sun is required to warm a needle-like leaf than a broad leaf. This benefits evergreen trees, which grow faster than deciduous trees in the boreal forest. In addition, soils in boreal forest regions tend to be acidic with little available nitrogen. Leaves are a nitrogen-rich structure and deciduous trees must produce a new set of these nitrogen-rich structures each year. Therefore, coniferous trees that retain nitrogen-rich needles may have a competitive advantage over the broad-leafed deciduous trees.

The net primary productivity of boreal forests is

lower than that of temperate forests and tropical wet forests. The above-ground biomass of boreal forests is high because these slow-growing tree species are long-lived and accumulate a large standing biomass over time. Plant species diversity is less than that seen in temperate forests and tropical wet forests. Boreal forests lack the pronounced elements of the layered forest structure seen in tropical wet forests. The structure of a boreal forest is often only a tree layer and a ground layer ([link]). When conifer needles are dropped, they decompose more slowly than broad leaves; therefore, fewer nutrients are returned to the soil to fuel plant growth.

Low-growing plants such as shrub willow dominate the tundra landscape, shown here in the Arctic National Wildlife Refuge. (credit: USFWS Arctic National Wildlife Refuge)

Arctic Tundra

The Arctic tundra lies north of the subarctic boreal forest and is located throughout the Arctic regions of the northern hemisphere ([link]). The average winter temperature is –34 °C (–29.2 °F) and the average summer temperature is from 3 °C to 12 °C (37 °F–52 °F). Plants in the arctic tundra have a very short growing season of approximately 10–12 weeks.

However, during this time, there are almost 24 hours of daylight and plant growth is rapid. The annual precipitation of the Arctic tundra is very low with little annual variation in precipitation. And, as in the boreal forests, there is little evaporation due to the cold temperatures.

Plants in the Arctic tundra are generally low to the ground ([link]). There is little species diversity, low net primary productivity, and low above-ground biomass. The soils of the Arctic tundra may remain in a perennially frozen state referred to as **permafrost**. The permafrost makes it impossible for roots to penetrate deep into the soil and slows the decay of organic matter, which inhibits the release of nutrients from organic matter. During the growing season, the ground of the Arctic tundra can be completely covered with plants or lichens.

Link to Learning

Watch this *Assignment Discovery: Biomes* video for an overview of biomes. To explore further, select one of the biomes on the extended playlist: desert, savanna, temperate forest, temperate grassland, tropic, tundra.

Section Summary

The Earth has terrestrial biomes and aquatic biomes. Aquatic biomes include both freshwater and marine environments. There are eight major terrestrial

biomes: tropical wet forests, savannas, subtropical deserts, chaparral, temperate grasslands, temperate forests, boreal forests, and Arctic tundra. The same biome can occur in different geographic locations with similar climates. Temperature and precipitation, and variations in both, are key abiotic factors that shape the composition of animal and plant communities in terrestrial biomes. Some biomes, such as temperate grasslands and temperate forests, have distinct seasons, with cold weather and hot weather alternating throughout the year. In warm, moist biomes, such as the tropical wet forest, net primary productivity is high, as warm temperatures, abundant water, and a year-round growing season fuel plant growth and supply energy for high diversity throughout the food web. Other biomes, such as deserts and tundras, have low primary productivity due to extreme temperatures and a shortage of available water.

Visual Connection Questions

[link] Which of the following statements about biomes is false?

1. Chaparral is dominated by shrubs.
2. Savannas and temperate grasslands are dominated by grasses.

3. Boreal forests are dominated by deciduous trees.
4. Lichens are common in the arctic tundra.

[link] C. Boreal forests are not dominated by deciduous trees.

Review Questions

Which of the following biomes is characterized by abundant water resources?

1. deserts
2. boreal forests
3. savannas
4. tropical wet forests

D

Which of the following biomes is characterized by short growing seasons?

1. deserts
2. tropical wet forests
3. Arctic tundras

4. savannas

C

Critical Thinking Questions

The extremely low precipitation of subtropical desert biomes might lead one to expect fire to be a major disturbance factor; however, fire is more common in the temperate grassland biome than in the subtropical desert biome. Why is this?

Fire is less common in desert biomes than in temperate grasslands because deserts have low net primary productivity and, thus, very little plant biomass to fuel a fire.

In what ways are the subtropical desert and the arctic tundra similar?

Both the subtropical desert and the arctic tundra have a low supply of water. In the desert, this is due to extremely low precipitation, and in the arctic tundra, much of

the water is unavailable to plants because it is frozen. Both the subtropical desert and the arctic tundra have low net primary productivity.

Glossary

canopy
: branches and foliage of trees that form a layer of overhead coverage in a forest

permafrost
: perennially frozen portion of the Arctic tundra soil

Aquatic and Marine Biomes

By the end of this section, you will be able to:

- Describe the effects of abiotic factors on the composition of plant and animal communities in aquatic biomes
- Compare the characteristics of the ocean zones
- Summarize the characteristics of standing water and flowing water in freshwater biomes

Like terrestrial biomes, aquatic biomes are influenced by abiotic factors. In the case of aquatic biomes the abiotic factors include light, temperature, flow regime, and dissolved solids. The aquatic medium—water— has different physical and chemical properties than air. Even if the water in a pond or other body of water is perfectly clear (there are no suspended particles), water, on its own, absorbs light. As one descends deep enough into a body of water, eventually there will be a depth at which the sunlight cannot reach. While there are some abiotic and biotic factors in a terrestrial ecosystem that shade light (like fog, dust, or insect swarms), these are not usually permanent features of the environment. The importance of light in aquatic biomes is central to the communities of organisms found in both freshwater and marine ecosystems because it controls productivity through photosynthesis.

In addition to light, solar radiation warms bodies of

water and many exhibit distinct layers of water at differing temperatures. The water temperature affects the organisms’ rates of growth and the amount of dissolved oxygen available for respiration.

The movement of water is also important in many aquatic biomes. In rivers, the organisms must obviously be adapted to the constant movement of the water around them, but even in larger bodies of water such as the oceans, regular currents and tides impact availability of nutrients, food resources, and the presence of the water itself.

Finally, all natural water contains dissolved solids, or salts. Fresh water contains low levels of such dissolved substances because the water is rapidly recycled through evaporation and precipitation. The oceans have a relatively constant high salt content. Aquatic habitats at the interface of marine and freshwater ecosystems have complex and variable salt environments that range between freshwater and marine levels. These are known as brackish water environments. Lakes located in closed drainage basins concentrate salt in their waters and can have extremely high salt content that only a few and highly specialized species are able to inhabit. Sea stars, sea urchins, and mussel shells are often found in the intertidal zone, shown here in Kachemak Bay, Alaska. (credit: NOAA) Coral reefs are formed by the calcium carbonate skeletons of

coral organisms, which are marine invertebrates in the phylum Cnidaria. (credit: Terry Hughes)

Marine Biomes

The ocean is a continuous body of salt water that is relatively uniform in chemical composition. It is a weak solution of mineral salts and decayed biological matter. Within the ocean, coral reefs are a second type of marine biome. Estuaries, coastal areas where salt water and fresh water mix, form a third unique marine biome.

The ocean is categorized by several zones ([link]). All of the ocean's open water is referred to as the **pelagic realm** (or zone). The **benthic realm** (or zone) extends along the ocean bottom from the shoreline to the deepest parts of the ocean floor. From the surface to the bottom or the limit to which photosynthesis occurs is the **photic zone** (approximately 200 m or 650 ft). At depths greater than 200 m, light cannot penetrate; thus, this is referred to as the **aphotic zone**. The majority of the ocean is aphotic and lacks sufficient light for photosynthesis. The deepest part of the ocean, the Challenger Deep (in the Mariana Trench, located in the western Pacific Ocean), is about 11,000 m (about 6.8 mi) deep. To give some perspective on the depth of this trench, the ocean is, on average, 4267 m or 14,000 ft deep.

Ocean

The physical diversity of the ocean has a significant influence on the diversity of organisms that live within it. The ocean is categorized into different zones based on how far light reaches into the water. Each zone has a distinct group of species adapted to the biotic and abiotic conditions particular to that zone.

The **intertidal zone** ([link]) is the oceanic region that is closest to land. With each tidal cycle, the intertidal zone alternates between being inundated with water and left high and dry. Generally, most people think of this portion of the ocean as a sandy beach. In some cases, the intertidal zone is indeed a sandy beach, but it can also be rocky, muddy, or dense with tangled roots in mangrove forests. The intertidal zone is an extremely variable environment because of tides. Organisms may be exposed to air at low tide and are underwater during high tide. Therefore, living things that thrive in the intertidal zone are often adapted to being dry for long periods of time. The shore of the intertidal zone is also repeatedly struck by waves and the organisms found there are adapted to withstand damage from the pounding action of the waves ([link]). The exoskeletons of shoreline crustaceans (such as the shore crab, *Carcinus maenas*) are tough and protect them from desiccation (drying out) and wave damage. Another consequence of the pounding

waves is that few algae and plants establish themselves in constantly moving sand or mud.

The **neritic zone** ([link]) extends from the margin of the intertidal zone to depths of about 200 m (or 650 ft) at the edge of the continental shelf. When the water is relatively clear, photosynthesis can occur in the neritic zone. The water contains silt and is well-oxygenated, low in pressure, and stable in temperature. These factors all contribute to the neritic zone having the highest productivity and biodiversity of the ocean. Phytoplankton, including photosynthetic bacteria and larger species of algae, are responsible for the bulk of this primary productivity. Zooplankton, protists, small fishes, and shrimp feed on the producers and are the primary food source for most of the world’s fisheries. The majority of these fisheries exist within the neritic zone.

Beyond the neritic zone is the open ocean area known as the **oceanic zone** ([link]). Within the oceanic zone there is thermal stratification. Abundant phytoplankton and zooplankton support populations of fish and whales. Nutrients are scarce and this is a relatively less productive part of the marine biome. When photosynthetic organisms and the organisms that feed on them die, their bodies fall to the bottom of the ocean where they remain; the open ocean lacks a process for bringing the organic nutrients back up to the surface.

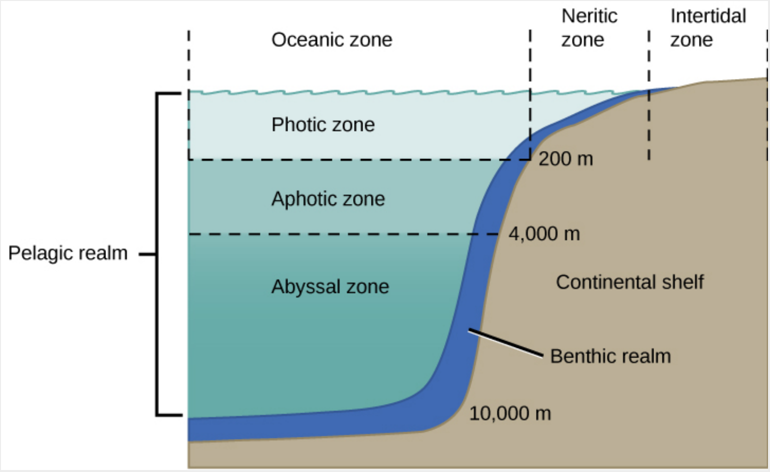
Beneath the pelagic zone is the benthic realm, the deepwater region beyond the continental shelf ([link]). The bottom of the benthic realm is comprised of sand, silt, and dead organisms. Temperature decreases as water depth increases. This is a nutrient-rich portion of the ocean because of the dead organisms that fall from the upper layers of the ocean. Because of this high level of nutrients, a diversity of fungi, sponges, sea anemones, marine worms, sea stars, fishes, and bacteria exists.

The deepest part of the ocean is the **abyssal zone**, which is at depths of 4000 m or greater. The abyssal zone ([link]) is very cold and has very high pressure, high oxygen content, and low nutrient content. There are a variety of invertebrates and fishes found in this zone, but the abyssal zone does not have photosynthetic organisms. Chemosynthetic bacteria use the hydrogen sulfide and other minerals

emitted from deep hydrothermal vents. These chemosynthetic bacteria use the hydrogen sulfide as an energy source and serve as the base of the food chain found around the vents.

Visual Connection

The ocean is divided into different zones based on water depth, distance from the shoreline, and light penetration.



In which of the following regions would you expect to find photosynthetic organisms?

1. The aphotic zone, the neritic zone, the oceanic zone, and the benthic realm.
2. The photic zone, the intertidal zone, the neritic zone, and the oceanic zone.
3. The photic zone, the abyssal zone, the neritic zone, and the oceanic zone.
4. The pelagic realm, the aphotic zone, the

neritic zone, and the oceanic zone.

Coral Reefs

Coral reefs are ocean ridges formed by marine invertebrates living in warm shallow waters within the photic zone of the ocean. They are found within 30° north and south of the equator. The Great Barrier Reef is a well-known reef system located several miles off the northeastern coast of Australia. Other coral reefs are fringing islands, which are directly adjacent to land, or atolls, which are circular reefs surrounding a former island that is now underwater. The coral-forming colonies of organisms (members of phylum Cnidaria) secrete a calcium carbonate skeleton. These calcium-rich skeletons slowly accumulate, thus forming the underwater reef ([link]). Corals found in shallower waters (at a depth of approximately 60 m or about 200 ft) have a mutualistic relationship with photosynthetic unicellular protists. The relationship provides corals with the majority of the nutrition and the energy they require. The waters in which these corals live are nutritionally poor and, without this mutualism, it would not be possible for large corals to grow because there are few planktonic organisms for them to feed on. Some corals living in deeper and colder water do not have a mutualistic relationship with protists; these corals must obtain

their energy exclusively by feeding on plankton using stinging cells on their tentacles.

Concept in Action

In this National Oceanic and Atmospheric Administration (NOAA) video, marine ecologist Dr. Peter Etnoyer discusses his research on coral organisms.

Coral reefs are one of the most diverse biomes. It is estimated that more than 4000 fish species inhabit coral reefs. These fishes can feed on coral, the **cryptofauna** (invertebrates found within the calcium carbonate structures of the coral reefs), or the seaweed and algae that are associated with the coral. These species include predators, herbivores, or planktivores. Predators are animal species that hunt and are carnivores or “flesh eaters.” Herbivores eat plant material, and **planktivores** eat plankton.

Evolution in Action

Global Decline of Coral Reefs

It takes a long time to build a coral reef. The animals that create coral reefs do so over

thousands of years, continuing to slowly deposit the calcium carbonate that forms their characteristic ocean homes. Bathed in warm tropical waters, the coral animals and their symbiotic protist partners evolved to survive at the upper limit of ocean water temperature.

Together, climate change and human activity pose dual threats to the long-term survival of the world's coral reefs. The main cause of killing of coral reefs is warmer-than-usual surface water. As global warming raises ocean temperatures, coral reefs are suffering. The excessive warmth causes the coral organisms to expel their endosymbiotic, food-producing protists, resulting in a phenomenon known as bleaching. The colors of corals are a result of the particular protist endosymbiont, and when the protists leave, the corals lose their color and turn white, hence the term "bleaching."

Rising levels of atmospheric carbon dioxide further threaten the corals in other ways; as carbon dioxide dissolves in ocean waters, it lowers pH, thus increasing ocean acidity. As acidity increases, it interferes with the calcification that normally occurs as coral animals build their calcium carbonate homes.

When a coral reef begins to die, species diversity plummets as animals lose food and shelter. Coral reefs are also economically important tourist destinations, so the decline of coral reefs poses a serious threat to coastal economies.

Human population growth has damaged corals in

other ways, too. As human coastal populations increase, the runoff of sediment and agricultural chemicals has increased, causing some of the once-clear tropical waters to become cloudy. At the same time, overfishing of popular fish species has allowed the predator species that eat corals to go unchecked.

Although a rise in global temperatures of 1°C–2°C (a conservative scientific projection) in the coming decades may not seem large, it is very significant to this biome. When change occurs rapidly, species can become extinct before evolution leads to newly adapted species. Many scientists believe that global warming, with its rapid (in terms of evolutionary time) and inexorable increases in temperature, is tipping the balance beyond the point at which many of the world's coral reefs can recover.

As estuary is where fresh water and salt water meet, such as the mouth of the Klamath River in California, shown here. (credit: U.S. Army Corps of Engineers)

Estuaries: Where the Ocean Meets Fresh Water

Estuaries are biomes that occur where a river, a source of fresh water, meets the ocean. Therefore, both fresh water and salt water are found in the

same vicinity; mixing results in a diluted (brackish) salt water. Estuaries form protected areas where many of the offspring of crustaceans, mollusks, and fish begin their lives. Salinity is an important factor that influences the organisms and the adaptations of the organisms found in estuaries. The salinity of estuaries varies and is based on the rate of flow of its freshwater sources. Once or twice a day, high tides bring salt water into the estuary. Low tides occurring at the same frequency reverse the current of salt water ([link]).

The daily mixing of fresh water and salt water is a physiological challenge for the plants and animals that inhabit estuaries. Many estuarine plant species are halophytes, plants that can tolerate salty conditions. Halophytic plants are adapted to deal with salt water spray and salt water on their roots. In some halophytes, filters in the roots remove the

salt from the water that the plant absorbs. Animals, such as mussels and clams (phylum Mollusca), have developed behavioral adaptations that expend a lot of energy to function in this rapidly changing environment. When these animals are exposed to low salinity, they stop feeding, close their shells, and switch from aerobic respiration (in which they use gills) to anaerobic respiration (a process that does not require oxygen). When high tide returns to the estuary, the salinity and oxygen content of the water increases, and these animals open their shells, begin feeding, and return to aerobic respiration.
The uncontrolled growth of algae in this waterway has resulted in an algal bloom.Rivers range from (a) narrow and shallow to (b) wide and slow moving. (credit a: modification of work by Cory Zanker; credit b: modification of work by David DeHetre)

Freshwater Biomes

Freshwater biomes include lakes, ponds, and wetlands (standing water) as well as rivers and streams (flowing water). Humans rely on freshwater biomes to provide aquatic resources for drinking water, crop irrigation, sanitation, recreation, and industry. These various roles and human benefits are referred to as **ecosystem services**. Lakes and ponds are found in terrestrial landscapes and are therefore connected with abiotic and biotic factors influencing these terrestrial biomes.

Lakes and Ponds

Lakes and ponds can range in area from a few square meters to thousands of square kilometers. Temperature is an important abiotic factor affecting living things found in lakes and ponds. During the summer in temperate regions, thermal stratification of deep lakes occurs when the upper layer of water is warmed by the Sun and does not mix with deeper, cooler water. The process produces a sharp transition between the warm water above and cold water beneath. The two layers do not mix until cooling temperatures and winds break down the stratification and the water in the lake mixes from top to bottom. During the period of stratification, most of the productivity occurs in the warm, well-illuminated, upper layer, while dead organisms slowly rain down into the cold, dark layer below where decomposing bacteria and cold-adapted species such as lake trout exist. Like the ocean, lakes and ponds have a photic layer in which photosynthesis can occur. Phytoplankton (algae and cyanobacteria) are found here and provide the base of the food web of lakes and ponds. Zooplankton, such as rotifers and small crustaceans, consume these phytoplankton. At the bottom of lakes and ponds, bacteria in the aphotic zone break down dead organisms that sink to the bottom.

Nitrogen and particularly phosphorus are important limiting nutrients in lakes and ponds. Therefore,

they are determining factors in the amount of phytoplankton growth in lakes and ponds. When there is a large input of nitrogen and phosphorus (e.g., from sewage and runoff from fertilized lawns and farms), the growth of algae skyrockets, resulting in a large accumulation of algae called an **algal bloom**. Algal blooms ([link]) can become so extensive that they reduce light penetration in water. As a result, the lake or pond becomes aphotic and photosynthetic plants cannot survive. When the algae die and decompose, severe oxygen depletion of the water occurs. Fishes and other organisms that require oxygen are then more likely to die.

Rivers and Streams

Rivers and the narrower streams that feed into the rivers are continuously moving bodies of water that carry water from the source or headwater to the mouth at a lake or ocean. The largest rivers include the Nile River in Africa, the Amazon River in South America, and the Mississippi River in North America ([link]).

(a) (b)

Abiotic features of rivers and streams vary along the length of the river or stream. Streams begin at a point of origin referred to as **source water**. The source water is usually cold, low in nutrients, and clear. The **channel** (the width of the river or stream) is narrower here than at any other place along the length of the river or stream. Headwater streams are of necessity at a higher elevation than the mouth of the river and often originate in regions with steep grades leading to higher flow rates than lower elevation stretches of the river.

Faster-moving water and the short distance from its origin results in minimal silt levels in headwater streams; therefore, the water is clear. Photosynthesis here is mostly attributed to algae that are growing on rocks; the swift current inhibits the growth of phytoplankton. Photosynthesis may be further reduced by tree cover reaching over the narrow stream. This shading also keeps temperatures lower. An additional input of energy can come from leaves or other organic material that falls into a river or stream from the trees and other plants that border the water. When the leaves decompose, the organic

material and nutrients in the leaves are returned to the water. The leaves also support a food chain of invertebrates that eat them and are in turn eaten by predatory invertebrates and fish. Plants and animals have adapted to this fast-moving water. For instance, leeches (phylum Annelida) have elongated bodies and suckers on both ends. These suckers attach to the substrate, keeping the leech anchored in place. In temperate regions, freshwater trout species (phylum Chordata) may be an important predator in these fast-moving and colder river and streams.

As the river or stream flows away from the source, the width of the channel gradually widens, the current slows, and the temperature characteristically increases. The increasing width results from the increased volume of water from more and more tributaries. Gradients are typically lower farther along the river, which accounts for the slowing flow. With increasing volume can come increased silt, and as the flow rate slows, the silt may settle, thus increasing the deposition of sediment. Phytoplankton can also be suspended in slow-moving water. Therefore, the water will not be as clear as it is near the source. The water is also warmer as a result of longer exposure to sunlight and the absence of tree cover over wider expanses between banks. Worms (phylum Annelida) and insects (phylum Arthropoda) can be found burrowing into the mud. Predatory vertebrates

(phylum Chordata) include waterfowl, frogs, and fishes. In heavily silt-laden rivers, these predators must find food in the murky waters, and, unlike the trout in the clear waters at the source, these vertebrates cannot use vision as their primary sense to find food. Instead, they are more likely to use taste or chemical cues to find prey.

When a river reaches the ocean or a large lake, the water typically slows dramatically and any silt in the river water will settle. Rivers with high silt content discharging into oceans with minimal currents and wave action will build deltas, low-elevation areas of sand and mud, as the silt settles onto the ocean bottom. Rivers with low silt content or in areas where ocean currents or wave action are high create estuarine areas where the fresh water and salt water mix.

Located in southern Florida, Everglades National Park is vast array of wetland environments, including sawgrass marshes, cypress swamps, and estuarine mangrove forests. Here, a great egret walks among cypress trees. (credit: NPS)

Wetlands

Wetlands are environments in which the soil is either permanently or periodically saturated with water. Wetlands are different from lakes and ponds because wetlands exhibit a near continuous cover of emergent vegetation. **Emergent vegetation** consists

of wetland plants that are rooted in the soil but have portions of leaves, stems, and flowers extending above the water’s surface. There are several types of wetlands including marshes, swamps, bogs, mudflats, and salt marshes ([link]).

Freshwater marshes and swamps are characterized by slow and steady water flow. Bogs develop in depressions where water flow is low or nonexistent. Bogs usually occur in areas where there is a clay bottom with poor percolation. Percolation is the movement of water through the pores in the soil or rocks. The water found in a bog is stagnant and oxygen depleted because the oxygen that is used during the decomposition of organic matter is not replaced. As the oxygen in the water is depleted, decomposition slows. This leads to organic acids and other acids building up and lowering the pH of the water. At a lower pH, nitrogen becomes unavailable

to plants. This creates a challenge for plants because nitrogen is an important limiting resource. Some types of bog plants (such as sundews, pitcher plants, and Venus flytraps) capture insects and extract the nitrogen from their bodies. Bogs have low net primary productivity because the water found in bogs has low levels of nitrogen and oxygen.

Section Summary

Aquatic biomes include both saltwater and freshwater biomes. The abiotic factors important for the structuring of aquatic biomes can be different than those seen in terrestrial biomes. Sunlight is an important factor in bodies of water, especially those that are very deep, because of the role of photosynthesis in sustaining certain organisms. Other important factors include temperature, water movement, and salt content. Oceans may be thought of as consisting of different zones based on water depth, distance from the shoreline, and light penetrance. Different kinds of organisms are adapted to the conditions found in each zone. Coral reefs are unique marine ecosystems that are home to a wide variety of species. Estuaries are found where rivers meet the ocean; their shallow waters provide nourishment and shelter for young crustaceans, mollusks, fishes, and many other species. Freshwater biomes include lakes, ponds, rivers, streams, and wetlands. Bogs are an interesting type of wetland

characterized by standing water, a lower pH, and a lack of nitrogen.

Art Connections

[link] In which of the following regions would you expect to find photosynthetic organisms?

1. The aphotic zone, the neritic zone, the oceanic zone, and the benthic realm.
2. The photic zone, the intertidal zone, the neritic zone, and the oceanic zone.
3. The photic zone, the abyssal zone, the neritic zone, and the oceanic zone.
4. The pelagic realm, the aphotic zone, the neritic zone, and the oceanic zone.

[link] B. The photic zone, the intertidal zone, the neritic zone, and the oceanic zone.

Multiple Choice

Where would you expect to find the most photosynthesis in an ocean biome?

1. aphotic zone
2. abyssal zone
3. benthic realm
4. intertidal zone

D

A key feature of estuaries is

1. low light conditions and high productivity
2. salt water and fresh water
3. frequent algal blooms
4. little or no vegetation

B

Free Response

Describe the conditions and challenges facing organisms living in the intertidal zone.

Organisms living in the intertidal zone must tolerate periodic exposure to air and sunlight and must be able to be periodically dry. They also must be able to endure the pounding

waves; for this reason, some shoreline organisms have hard exoskeletons that provide protection while also reducing the likelihood of drying out.

Glossary

abyssal zone
: the deepest part of the ocean at depths of 4000 m or greater

algal bloom
: a rapid increase of algae in an aquatic system

aphotic zone
: the part of the ocean where photosynthesis cannot occur

benthic realm
: (also, benthic zone) the part of the ocean that extends along the ocean bottom from the shoreline to the deepest parts of the ocean floor

channel
: the bed and banks of a river or stream

coral reef
: an ocean ridge formed by marine invertebrates living in warm shallow waters within the photic zone

cryptofauna

the invertebrates found within the calcium carbonate substrate of coral reefs

ecosystem services

the human benefits provided by natural ecosystems

emergent vegetation

the plants living in bodies of water that are rooted in the soil but have portions of leaves, stems, and flowers extending above the water's surface

estuary

a region where fresh water and salt water mix where a river discharges into an ocean or sea

intertidal zone

the part of the ocean that is closest to land; parts extend above the water at low tide

neritic zone

the part of the ocean that extends from low tide to the edge of the continental shelf

oceanic zone

the part of the ocean that begins offshore where the water measures 200 m deep or deeper

pelagic realm

(also, pelagic zone) the open ocean waters that are not close to the bottom or near the shore

photic zone
: the upper layer of ocean water in which photosynthesis is able to take place

planktivore
: an animal that eats plankton

source water
: the point of origin of a river or stream

wetland
: environment in which the soil is either permanently or periodically saturated with water

Importance of Biodiversity

By the end of this section, you will be able to:

- Describe biodiversity as the equilibrium of naturally fluctuating rates of extinction and speciation
- Identify benefits of biodiversity to humans

This tropical lowland rainforest in Madagascar is an example of a high biodiversity habitat. This particular location is protected within a national forest, yet only 10 percent of the original coastal lowland forest remains, and research suggests half the original biodiversity has been lost. (credit: Frank Vassen)

Biodiversity is a broad term for biological variety,

and it can be measured at a number of organizational levels. Traditionally, ecologists have measured **biodiversity** by taking into account both the number of species and the number of individuals in each of those species. However, biologists are using measures of biodiversity at several levels of biological organization (including genes, populations, and ecosystems) to help focus efforts to preserve the biologically and technologically important elements of biodiversity.

When biodiversity loss through extinction is thought of as the loss of the passenger pigeon, the dodo, or, even, the woolly mammoth there seems to be no reason to care about it because these events happened long ago. How is the loss practically important for the welfare of the human species? Would these species have made our lives any better? From the perspective of evolution and ecology, the loss of a particular individual species, with some exceptions, may seem unimportant, but the current accelerated extinction rate means the loss of tens of thousands of species within our lifetimes. Much of this loss is occurring in tropical rainforests like the one pictured in [link], which are especially high-diversity ecosystems that are being cleared for timber and agriculture. This is likely to have dramatic effects on human welfare through the collapse of ecosystems and in added costs to maintain food production, clean air and water, and improve human health.

Biologists recognize that human populations are embedded in ecosystems and are dependent on them, just as is every other species on the planet. Agriculture began after early hunter-gatherer societies first settled in one place and heavily modified their immediate environment: the ecosystem in which they existed. This cultural transition has made it difficult for humans to recognize their dependence on living things other than crops and domesticated animals on the planet. Today our technology smoothes out the extremes of existence and allows many of us to live longer, more comfortable lives, but ultimately the human species cannot exist without its surrounding ecosystems. Our ecosystems provide our food. This includes living plants that grow in soil ecosystems and the animals that eat these plants (or other animals) as well as photosynthetic organisms in the oceans and the other organisms that eat them. Our ecosystems have provided and will provide many of the medications that maintain our health, which are commonly made from compounds found in living organisms. Ecosystems provide our clean water, which is held in lake and river ecosystems or passes through terrestrial ecosystems on its way into groundwater.

The variety of ecosystems on Earth—from coral reef to prairie—enables a great diversity of species to exist. (credit "coral reef": modification of work by Jim Maragos, USFWS; credit: "prairie": modification of work by Jim Minnerath, USFWS)International

Institute for Species Exploration (IISE), *2011 State of Observed Species (SOS)*. Tempe, AZ: IISE, 2011. Accessed May, 20, 2012. http://species.asu.edu/SOS.

Types of Biodiversity

A common meaning of biodiversity is simply the number of species in a location or on Earth; for example, the American Ornithologists' Union lists 2078 species of birds in North and Central America. This is one measure of the bird biodiversity on the continent. More sophisticated measures of diversity take into account the relative abundances of species. For example, a forest with 10 equally common species of trees is more diverse than a forest that has 10 species of trees wherein just one of those species makes up 95 percent of the trees rather than them being equally distributed. Biologists have also identified alternate measures of biodiversity, some of which are important in planning how to preserve biodiversity.

Genetic and Chemical Biodiversity

Genetic diversity is one alternate concept of biodiversity. **Genetic diversity** (or variation) is the raw material for adaptation in a species. A species' future potential for adaptation depends on the genetic diversity held in the genomes of the

individuals in populations that make up the species. The same is true for higher taxonomic categories. A genus with very different types of species will have more genetic diversity than a genus with species that look alike and have similar ecologies. The genus with the greatest potential for subsequent evolution is the most genetically diverse one.

Most genes code for proteins, which in turn carry out the metabolic processes that keep organisms alive and reproducing. Genetic diversity can also be conceived of as **chemical diversity** in that species with different genetic makeups produce different assortments of chemicals in their cells (proteins as well as the products and byproducts of metabolism). This chemical diversity is important for humans because of the potential uses for these chemicals, such as medications. For example, the drug eptifibatide is derived from rattlesnake venom and is used to prevent heart attacks in individuals with certain heart conditions.

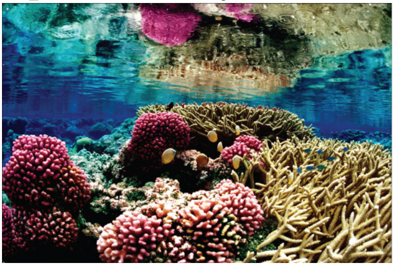
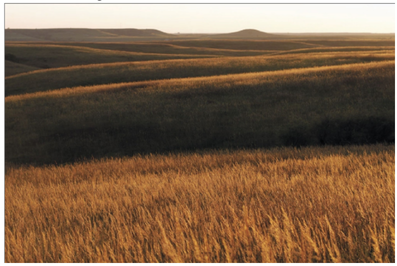
At present, it is far cheaper to discover compounds made by an organism than to imagine them and then synthesize them in a laboratory. Chemical diversity is one way to measure diversity that is important to human health and welfare. Through selective breeding, humans have domesticated animals, plants, and fungi, but even this diversity is suffering losses because of market forces and increasing globalism in human agriculture and

migration. For example, international seed companies produce only a very few varieties of a given crop and provide incentives around the world for farmers to buy these few varieties while abandoning their traditional varieties, which are far more diverse. The human population depends on crop diversity directly as a stable food source and its decline is troubling to biologists and agricultural scientists.

Ecosystems Diversity

It is also useful to define **ecosystem diversity**: the number of different ecosystems on Earth or in a geographical area. Whole ecosystems can disappear even if some of the species might survive by adapting to other ecosystems. The loss of an ecosystem means the loss of the interactions between species, the loss of unique features of coadaptation, and the loss of biological productivity that an ecosystem is able to create. An example of a largely extinct ecosystem in North America is the prairie ecosystem ([link]). Prairies once spanned central North America from the boreal forest in northern Canada down into Mexico. They are now all but gone, replaced by crop fields, pasture lands, and suburban sprawl. Many of the species survive, but the hugely productive ecosystem that was responsible for creating our most productive agricultural soils is now gone. As a consequence, their soils are now being depleted unless they are

maintained artificially at greater expense. The decline in soil productivity occurs because the interactions in the original ecosystem have been lost; this was a far more important loss than the relatively few species that were driven extinct when the prairie ecosystem was destroyed.

Current Species Diversity

Despite considerable effort, knowledge of the species that inhabit the planet is limited. A recent estimate suggests that the eukaryote species for which science has names, about 1.5 million species, account for less than 20 percent of the total number of eukaryote species present on the planet (8.7 million species, by one estimate). Estimates of numbers of prokaryotic species are largely guesses, but biologists agree that science has only just begun to catalog their diversity. Even with what is known, there is no centralized repository of names or samples of the described species; therefore, there is no way to be sure that the 1.5 million descriptions is an accurate number. It is a best guess based on the opinions of experts on different taxonomic groups. Given that Earth is losing species at an accelerating

pace, science knows little about what is being lost. [link] presents recent estimates of biodiversity in different groups.

Estimated Numbers of Described and Predicted species						
	Source: Mora et al 2011		**Source: Chapman 2009**		**Source: Groombridge and Jenkins 2002**	
	Described	Predicted	Described	Predicted	Described	Predicted
Animals	1,124,516	9,920,000	1,424,153	6,836,330	1,225,500	10,820,000
Photosynthetic protists	17,892	34,900	25,044	200,500	—	—
Fungi	44,368	616,320	98,998	1,500,000	72,000	1,500,000
Plants	224,244	314,600	310,129	390,800	270,000	320,000
Non-photosynthetic protists	16,236	72,800	28,871	1,000,000	80,000	600,000
Prokaryotes			10,307	1,000,000	10,175	
Total	1,438,769	10,960,000	1,897,502	10,897,630	1,657,675	13,240,000

This table shows the estimated number of species by taxonomic group—including both described (named and studied) and predicted (yet to be named) species.

There are various initiatives to catalog described species in accessible and more organized ways, and the internet is facilitating that effort. Nevertheless, at the current rate of species description, which according to the State of Observed Species[footnote] reports is 17,000–20,000 new species a year, it would take close to 500 years to describe all of the species currently in existence. The task, however, is becoming increasingly impossible over time as **extinction** removes species from Earth faster than they can be described.

Naming and counting species may seem an unimportant pursuit given the other needs of humanity, but it is not simply an accounting. Describing species is a complex process by which biologists determine an organism's unique characteristics and whether or not that organism belongs to any other described species. It allows biologists to find and recognize the species after the initial discovery to follow up on questions about its biology. That subsequent research will produce the discoveries that make the species valuable to humans and to our ecosystems. Without a name and description, a species cannot be studied in depth and in a coordinated way by multiple scientists.

This map illustrates the number of amphibian species across the globe and shows the trend toward higher biodiversity at lower latitudes. A similar pattern is observed for most taxonomic groups.

Patterns of Biodiversity

Biodiversity is not evenly distributed on the planet. Lake Victoria contained almost 500 species of cichlids (only one family of fishes present in the lake) before the introduction of an exotic species in the 1980s and 1990s caused a mass extinction. All of these species were found only in Lake Victoria, which is to say they were endemic. **Endemic species** are found in only one location. For example, the blue jay is endemic to North America, while the Barton Springs salamander is endemic to the mouth of one spring in Austin, Texas. Endemics with highly restricted distributions, like the Barton Springs salamander, are particularly vulnerable to extinction. Higher taxonomic levels, such as genera and families, can also be endemic.

Lake Huron contains about 79 species of fish, all of which are found in many other lakes in North America. What accounts for the difference in diversity between Lake Victoria and Lake Huron? Lake Victoria is a tropical lake, while Lake Huron is a temperate lake. Lake Huron in its present form is only about 7,000 years old, while Lake Victoria in its present form is about 15,000 years old. These

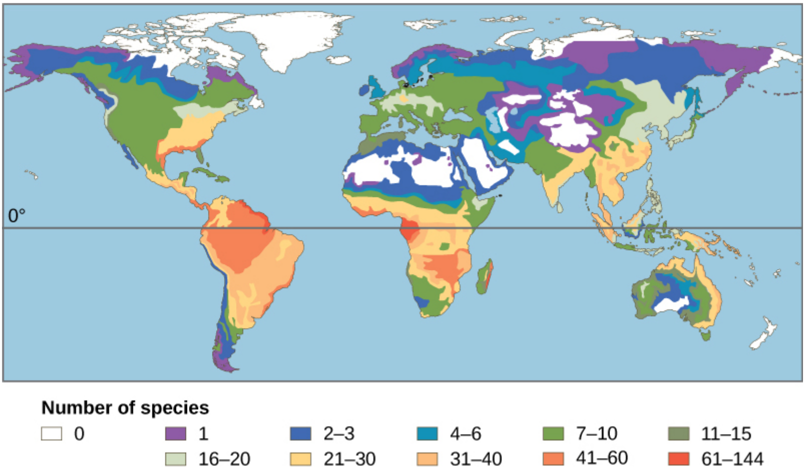
two factors, latitude and age, are two of several hypotheses biogeographers have suggested to explain biodiversity patterns on Earth.

Career in Action

Biogeography

Biogeography is the study of the distribution of the world’s species both in the past and in the present. The work of biogeographers is critical to understanding our physical environment, how the environment affects species, and how changes in environment impact the distribution of a species. There are three main fields of study under the heading of biogeography: ecological biogeography, historical biogeography (called paleobiogeography), and conservation biogeography. Ecological biogeography studies the current factors affecting the distribution of plants and animals. Historical biogeography, as the name implies, studies the past distribution of species. Conservation biogeography, on the other hand, is focused on the protection and restoration of species based upon the known historical and current ecological information. Each of these fields considers both zoogeography and phytogeography—the past and present distribution of animals and plants.

One of the oldest observed patterns in ecology is that biodiversity in almost every taxonomic group of organism increases as latitude declines. In other words, biodiversity increases closer to the equator ([link]).



It is not yet clear why biodiversity increases closer to the equator, but hypotheses include the greater age of the ecosystems in the tropics versus temperate regions, which were largely devoid of life or drastically impoverished during the last ice age. The greater age provides more time for speciation. Another possible explanation is the greater energy the tropics receive from the sun versus the lesser energy input in temperate and polar regions. But scientists have not been able to explain how greater energy input could translate into more species. The complexity of tropical ecosystems may promote speciation by increasing the **habitat heterogeneity**, or number of ecological niches, in the tropics relative to higher latitudes. The greater

heterogeneity provides more opportunities for coevolution, specialization, and perhaps greater selection pressures leading to population differentiation. However, this hypothesis suffers from some circularity—ecosystems with more species encourage speciation, but how did they get more species to begin with? The tropics have been perceived as being more stable than temperate regions, which have a pronounced climate and day-length seasonality. The tropics have their own forms of seasonality, such as rainfall, but they are generally assumed to be more stable environments and this stability might promote speciation.

Regardless of the mechanisms, it is certainly true that biodiversity is greatest in the tropics. The number of endemic species is higher in the tropics. The tropics also contain more biodiversity hotspots. At the same time, our knowledge of the species living in the tropics is lowest and because of recent, heavy human activity the potential for biodiversity loss is greatest.

Catharanthus roseus, the Madagascar periwinkle, has various medicinal properties. Among other uses, it is a source of vincristine, a drug used in the treatment of lymphomas. (credit: Forest and Kim Starr)

Importance of Biodiversity

Loss of biodiversity eventually threatens other species we do not impact directly because of their

interconnectedness; as species disappear from an ecosystem other species are threatened by the changes in available resources. Biodiversity is important to the survival and welfare of human populations because it has impacts on our health and our ability to feed ourselves through agriculture and harvesting populations of wild animals.

Human Health

Many medications are derived from natural chemicals made by a diverse group of organisms. For example, many plants produce **secondary plant compounds**, which are toxins used to protect the plant from insects and other animals that eat them. Some of these secondary plant compounds also work as human medicines. Contemporary societies that live close to the land often have a broad knowledge of the medicinal uses of plants growing in their area. For centuries in Europe, older knowledge about the medical uses of plants was compiled in herbals—books that identified the plants and their uses. Humans are not the only animals to use plants for medicinal reasons. The other great apes, orangutans, chimpanzees, bonobos, and gorillas have all been observed self-medicating with plants.

Modern pharmaceutical science also recognizes the importance of these plant compounds. Examples of significant medicines derived from plant compounds include aspirin, codeine, digoxin, atropine, and

vincristine ([link]). Many medications were once derived from plant extracts but are now synthesized. It is estimated that, at one time, 25 percent of modern drugs contained at least one plant extract. That number has probably decreased to about 10 percent as natural plant ingredients are replaced by synthetic versions of the plant compounds. Antibiotics, which are responsible for extraordinary improvements in health and lifespans in developed countries, are compounds largely derived from fungi and bacteria.

In recent years, animal venoms and poisons have excited intense research for their medicinal potential. By 2007, the FDA had approved five drugs based on animal toxins to treat diseases such as hypertension, chronic pain, and diabetes. Another five drugs are undergoing clinical trials and at least six drugs are being used in other countries. Other

toxins under investigation come from mammals, snakes, lizards, various amphibians, fish, snails, octopuses, and scorpions.

Aside from representing billions of dollars in profits, these medications improve people's lives. Pharmaceutical companies are actively looking for new natural compounds that can function as medicines. It is estimated that one third of pharmaceutical research and development is spent on natural compounds and that about 35 percent of new drugs brought to market between 1981 and 2002 were from natural compounds.

Finally, it has been argued that humans benefit psychologically from living in a biodiverse world. The chief proponent of this idea is entomologist E. O. Wilson. He argues that human evolutionary history has adapted us to living in a natural environment and that built environments generate stresses that affect human health and well-being. There is considerable research into the psychologically regenerative benefits of natural landscapes that suggest the hypothesis may hold some truth.

Agricultural

Since the beginning of human agriculture more than 10,000 years ago, human groups have been breeding and selecting crop varieties. This crop

diversity matched the cultural diversity of highly subdivided populations of humans. For example, potatoes were domesticated beginning around 7,000 years ago in the central Andes of Peru and Bolivia. The people in this region traditionally lived in relatively isolated settlements separated by mountains. The potatoes grown in that region belong to seven species and the number of varieties likely is in the thousands. Each variety has been bred to thrive at particular elevations and soil and climate conditions. The diversity is driven by the diverse demands of the dramatic elevation changes, the limited movement of people, and the demands created by crop rotation for different varieties that will do well in different fields.

Potatoes are only one example of agricultural diversity. Every plant, animal, and fungus that has been cultivated by humans has been bred from original wild ancestor species into diverse varieties arising from the demands for food value, adaptation to growing conditions, and resistance to pests. The potato demonstrates a well-known example of the risks of low crop diversity: during the tragic Irish potato famine (1845–1852 AD), the single potato variety grown in Ireland became susceptible to a potato blight—wiping out the crop. The loss of the crop led to famine, death, and mass emigration. Resistance to disease is a chief benefit to maintaining crop biodiversity and lack of diversity in contemporary crop species carries similar risks.

Seed companies, which are the source of most crop varieties in developed countries, must continually breed new varieties to keep up with evolving pest organisms. These same seed companies, however, have participated in the decline of the number of varieties available as they focus on selling fewer varieties in more areas of the world replacing traditional local varieties.

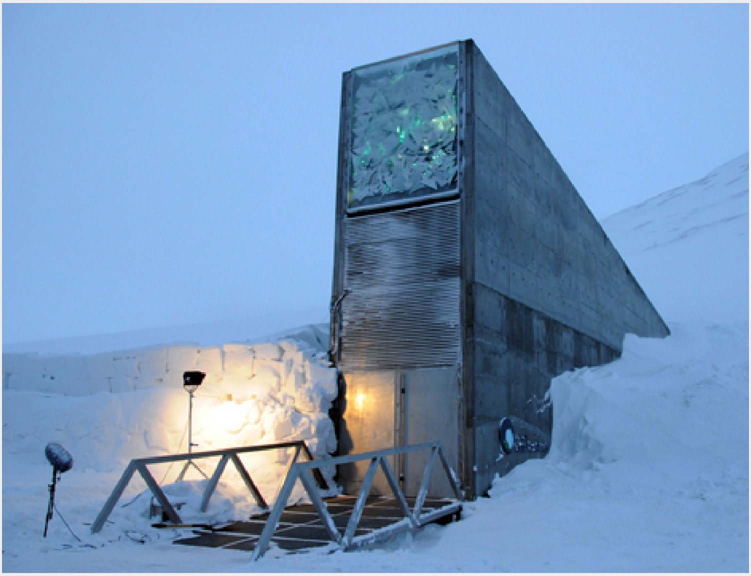
The ability to create new crop varieties relies on the diversity of varieties available and the availability of wild forms related to the crop plant. These wild forms are often the source of new gene variants that can be bred with existing varieties to create varieties with new attributes. Loss of wild species related to a crop will mean the loss of potential in crop improvement. Maintaining the genetic diversity of wild species related to domesticated species ensures our continued supply of food.

Since the 1920s, government agriculture departments have maintained seed banks of crop varieties as a way to maintain crop diversity. This system has flaws because over time seed varieties are lost through accidents and there is no way to replace them. In 2008, the Svalbard Global seed Vault, located on Spitsbergen island, Norway, ([link]) began storing seeds from around the world as a backup system to the regional seed banks. If a regional seed bank stores varieties in Svalbard, losses can be replaced from Svalbard should

something happen to the regional seeds. The Svalbard seed vault is deep into the rock of the arctic island. Conditions within the vault are maintained at ideal temperature and humidity for seed survival, but the deep underground location of the vault in the arctic means that failure of the vault's systems will not compromise the climatic conditions inside the vault.

Visual Connection

The Svalbard Global Seed Vault is a storage facility for seeds of Earth's diverse crops. (credit: Mari Tefre, Svalbard Global Seed Vault)



The Svalbard seed vault is located on Spitsbergen island in Norway, which has an arctic climate. Why might an arctic climate be good for seed storage?

Although crops are largely under our control, our ability to grow them is dependent on the biodiversity of the ecosystems in which they are grown. That biodiversity creates the conditions under which crops are able to grow through what are known as ecosystem services—valuable conditions or processes that are carried out by an ecosystem. Crops are not grown, for the most part, in built environments. They are grown in soil. Although some agricultural soils are rendered sterile using controversial pesticide treatments, most contain a huge diversity of organisms that maintain nutrient cycles—breaking down organic matter into nutrient compounds that crops need for growth. These organisms also maintain soil texture that affects water and oxygen dynamics in the soil that are necessary for plant growth. Replacing the work of these organisms in forming arable soil is not practically possible. These kinds of processes are called ecosystem services. They occur within ecosystems, such as soil ecosystems, as a result of the diverse metabolic activities of the organisms living there, but they provide benefits to human food production, drinking water availability, and breathable air.

Other key ecosystem services related to food production are plant pollination and crop pest control. It is estimated that honeybee pollination within the United States brings in $1.6 billion per year; other pollinators contribute up to $6.7 billion.

Over 150 crops in the United States require pollination to produce. Many honeybee populations are managed by beekeepers who rent out their hives' services to farmers. Honeybee populations in North America have been suffering large losses caused by a syndrome known as colony collapse disorder, a new phenomenon with an unclear cause. Other pollinators include a diverse array of other bee species and various insects and birds. Loss of these species would make growing crops requiring pollination impossible, increasing dependence on other crops.

Finally, humans compete for their food with crop pests, most of which are insects. Pesticides control these competitors, but these are costly and lose their effectiveness over time as pest populations adapt. They also lead to collateral damage by killing non-pest species as well as beneficial insects like honeybees, and risking the health of agricultural workers and consumers. Moreover, these pesticides may migrate from the fields where they are applied and do damage to other ecosystems like streams, lakes, and even the ocean. Ecologists believe that the bulk of the work in removing pests is actually done by predators and parasites of those pests, but the impact has not been well studied. A review found that in 74 percent of studies that looked for an effect of landscape complexity (forests and fallow fields near to crop fields) on natural enemies of pests, the greater the complexity, the greater the

effect of pest-suppressing organisms. Another experimental study found that introducing multiple enemies of pea aphids (an important alfalfa pest) increased the yield of alfalfa significantly. This study shows that a diversity of pests is more effective at control than one single pest. Loss of diversity in pest enemies will inevitably make it more difficult and costly to grow food. The world's growing human population faces significant challenges in the increasing costs and other difficulties associated with producing food.

Wild Food Sources

In addition to growing crops and raising food animals, humans obtain food resources from wild populations, primarily wild fish populations. For about one billion people, aquatic resources provide the main source of animal protein. But since 1990, production from global fisheries has declined. Despite considerable effort, few fisheries on Earth are managed sustainability.

Fishery extinctions rarely lead to complete extinction of the harvested species, but rather to a radical restructuring of the marine ecosystem in which a dominant species is so over-harvested that it becomes a minor player, ecologically. In addition to humans losing the food source, these alterations affect many other species in ways that are difficult or impossible to predict. The collapse of fisheries

has dramatic and long-lasting effects on local human populations that work in the fishery. In addition, the loss of an inexpensive protein source to populations that cannot afford to replace it will increase the cost of living and limit societies in other ways. In general, the fish taken from fisheries have shifted to smaller species and the larger species are overfished. The ultimate outcome could clearly be the loss of aquatic systems as food sources.

Concept in Action

Visit this website to view a brief video discussing a study of declining fisheries.

Section Summary

Biodiversity exists at multiple levels of organization, and is measured in different ways depending on the goals of those taking the measurements. These include numbers of species, genetic diversity, chemical diversity, and ecosystem diversity. The number of described species is estimated to be 1.5 million with about 17,000 new species being described each year. Estimates for the total number of eukaryotic species on Earth vary but are on the

order of 10 million. Biodiversity is negatively correlated with latitude for most taxa, meaning that biodiversity is higher in the tropics. The mechanism for this pattern is not known with certainty, but several plausible hypotheses have been advanced.

Humans use many compounds that were first discovered or derived from living organisms as medicines: secondary plant compounds, animal toxins, and antibiotics produced by bacteria and fungi. More medicines are expected to be discovered in nature. Loss of biodiversity will impact the number of pharmaceuticals available to humans. Biodiversity may provide important psychological benefits to humans.

Crop diversity is a requirement for food security, and it is being lost. The loss of wild relatives to crops also threatens breeders' abilities to create new varieties. Ecosystems provide ecosystem services that support human agriculture: pollination, nutrient cycling, pest control, and soil development and maintenance. Loss of biodiversity threatens these ecosystem services and risks making food production more expensive or impossible. Wild food sources are mainly aquatic, but few are being managed for sustainability. Fisheries' ability to provide protein to human populations is threatened when extinction occurs.

Art Connections

[link] The Svalbard seed vault is located on Spitsbergen island in Norway, which has an arctic climate. Why might an arctic climate be good for seed storage?

[link] The ground is permanently frozen so the seeds will keep, even if the electricity fails.

Multiple Choice

The number of currently described species on the planet is about ______.

1. 17,000
2. 150,000
3. 1.5 million
4. 10 million

C

A secondary plant compound might be used for which of the following?

1. a new crop variety
2. a new drug
3. a soil nutrient
4. a crop pest

B

Pollination is an example of _____.

1. a possible source of new drugs
2. chemical diversity
3. an ecosystem service
4. crop pest control

C

Free Response

Explain how biodiversity loss can impact crop diversity.

Crop plants are derived from wild plants, and genes from wild relatives are frequently brought into crop varieties by plant breeders to add valued characteristics to the crops. If the

wild species are lost, then this genetic variation would no longer be available.

Describe two types of compounds from living things that are used as medications.

Secondary plant compounds are toxins produced by plants to kill predators trying to eat them; some of these compounds can be used as drugs. Animal toxins, such as snake venom, can be used as medicine. (Alternate answer: antibiotics are compounds produced by bacteria and fungi which can be used to kill bacteria.)

Glossary

biodiversity
: the variety of a biological system, typically conceived as the number of species, but also applying to genes, biochemistry, and ecosystems

chemical diversity
: the variety of metabolic compounds in an ecosystem

ecosystem diversity
: the variety of ecosystems

endemic species
: a species native to one place

extinction
: the disappearance of a species from Earth; local extinction is the disappearance of a species from a region

genetic diversity
: the variety of genes and alleles in a species or other taxonomic group or ecosystem; the term can refer to allelic diversity or genome-wide diversity

habitat heterogeneity
: the number of ecological niches

secondary plant compound
: a compound produced as a byproduct of plant metabolic processes that is typically toxic, but is sequestered by the plant to defend against herbivores

Threats to Biodiversity

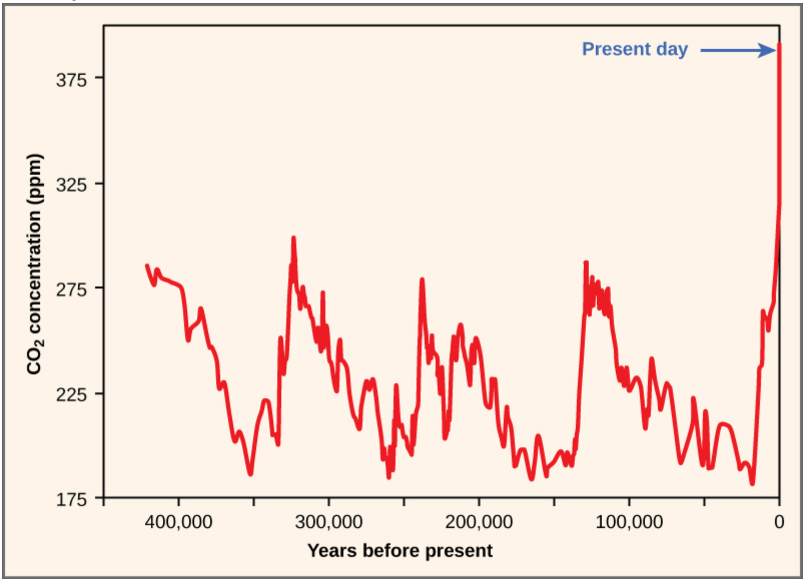
By the end of this section, you will be able to:

- Identify significant threats to biodiversity
- Explain the effects of habitat loss, exotic species, and hunting on biodiversity
- Identify the early and predicted effects of climate change on biodiversity

The core threat to biodiversity on the planet, and therefore a threat to human welfare, is the combination of human population growth and resource exploitation. The human population requires resources to survive and grow, and those resources are being removed unsustainably from the environment. The three greatest proximate threats to biodiversity are habitat loss, overharvesting, and introduction of exotic species. The first two of these are a direct result of human population growth and resource use. The third results from increased mobility and trade. A fourth major cause of extinction, anthropogenic climate change, has not yet had a large impact, but it is predicted to become significant during this century. Global climate change is also a consequence of human population needs for energy and the use of fossil fuels to meet those needs ([link]). Environmental issues, such as toxic pollution, have specific targeted effects on species, but they are not generally seen as threats at the magnitude of the others.

Atmospheric carbon dioxide levels fluctuate in a

cyclical manner. However, the burning of fossil fuels in recent history has caused a dramatic increase in the levels of carbon dioxide in the Earth's atmosphere, which have now reached levels never before seen in human history. Scientists predict that the addition of this "greenhouse gas" to the atmosphere is resulting in climate change that will significantly impact biodiversity in the coming century.



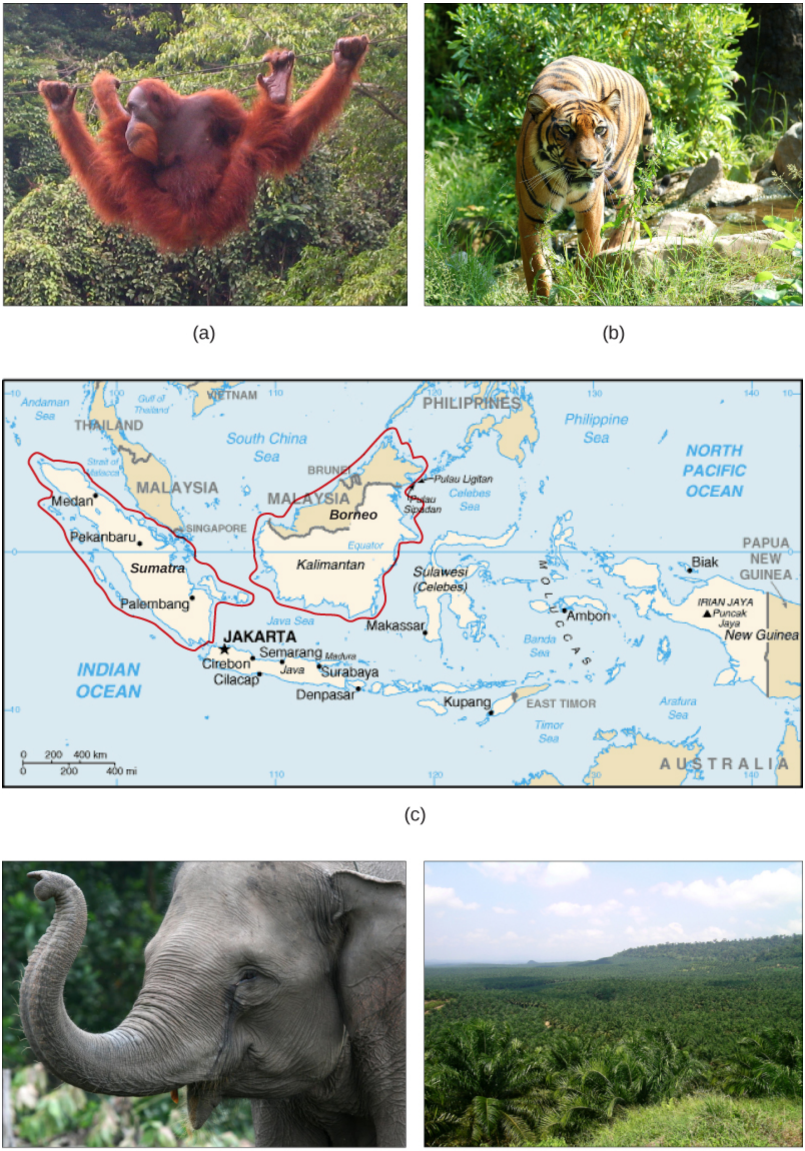
(a) One species of orangutan, *Pongo pygmaeus,* is found only in the rainforests of Borneo, and the other species of orangutan (*Pongo abelii*) is found only in the rainforests of Sumatra. These animals are examples of the exceptional biodiversity of (c) the islands of Sumatra and Borneo. Other species include the (b) Sumatran tiger (*Panthera tigris sumatrae*) and the (d) Sumatran elephant (*Elephas maximus sumatranus*), both critically endangered

species. Rainforest habitat is being removed to make way for (e) oil palm plantations such as this one in Borneo’s Sabah Province. (credit a: modification of work by Thorsten Bachner; credit b: modification of work by Dick Mudde; credit c: modification of work by U.S. CIA World Factbook; credit d: modification of work by “Nonprofit Organizations”/Flickr; credit e: modification of work by Dr. Lian Pin Koh)

Habitat Loss

Humans rely on technology to modify their environment and replace certain functions that were once performed by the natural ecosystem. Other species cannot do this. Elimination of their ecosystem—whether it is a forest, a desert, a grassland, a freshwater estuarine, or a marine environment—will kill the individuals in the species. Remove the entire habitat within the range of a species and, unless they are one of the few species that do well in human-built environments, the species will become extinct. Human destruction of habitats accelerated in the latter half of the twentieth century. Consider the exceptional biodiversity of Sumatra: it is home to one species of orangutan, a species of critically endangered elephant, and the Sumatran tiger, but half of Sumatra’s forest is now gone. The neighboring island of Borneo, home to the other species of orangutan, has lost a similar area of forest. Forest loss continues in protected areas of Borneo. The

orangutan in Borneo is listed as endangered by the International Union for Conservation of Nature (IUCN), but it is simply the most visible of thousands of species that will not survive the disappearance of the forests of Borneo. The forests are removed for timber and to plant palm oil plantations ([link]). Palm oil is used in many products including food products, cosmetics, and biodiesel in Europe. A five-year estimate of global forest cover loss for the years 2000–2005 was 3.1 percent. In the humid tropics where forest loss is primarily from timber extraction, 272,000 km^2 was lost out of a global total of 11,564,000 km^2 (or 2.4 percent). In the tropics, these losses certainly also represent the extinction of species because of high levels of endemism.



(a) (b) (c) (d) (e)

Everyday Connection

Preventing Habitat Destruction with Wise Wood

Choices

Most consumers do not imagine that the home improvement products they buy might be contributing to habitat loss and species extinctions. Yet the market for illegally harvested tropical timber is huge, and the wood products often find themselves in building supply stores in the United States. One estimate is that 10 percent of the imported timber stream in the United States, which is the world's largest consumer of wood products, is potentially illegally logged. In 2006, this amounted to $3.6 billion in wood products. Most of the illegal products are imported from countries that act as intermediaries and are not the originators of the wood.

How is it possible to determine if a wood product, such as flooring, was harvested sustainably or even legally? The Forest Stewardship Council (FSC) certifies sustainably harvested forest products, therefore, looking for their certification on flooring and other hardwood products is one way to ensure that the wood has not been taken illegally from a tropical forest. Certification applies to specific products, not to a producer; some producers' products may not have certification while other products are certified. While there are other industry-backed certifications other than the FSC, these are unreliable due to lack of independence from the industry. Another approach is to buy domestic wood species. While it would be great if there was a list of legal versus illegal wood

products, it is not that simple. Logging and forest management laws vary from country to country; what is illegal in one country may be legal in another. Where and how a product is harvested and whether the forest from which it comes is being maintained sustainably all factor into whether a wood product will be certified by the FSC. It is always a good idea to ask questions about where a wood product came from and how the supplier knows that it was harvested legally.

Habitat destruction can affect ecosystems other than forests. Rivers and streams are important ecosystems and are frequently modified through land development and from damming or water removal. Damming of rivers affects the water flow and access to all parts of a river. Differing flow regimes can reduce or eliminate populations that are adapted to these changes in flow patterns. For example, an estimated 91percent of river lengths in the United States have been developed: they have modifications like dams, to create energy or store water; levees, to prevent flooding; or dredging or rerouting, to create land that is more suitable for human development. Many fish species in the United States, especially rare species or species with restricted distributions, have seen declines caused by river damming and habitat loss. Research has confirmed that species of amphibians that must carry out parts of their life

cycles in both aquatic and terrestrial habitats have a greater chance of suffering population declines and extinction because of the increased likelihood that one of their habitats or access between them will be lost.

Overharvesting

Overharvesting is a serious threat to many species, but particularly to aquatic species. There are many examples of regulated commercial fisheries monitored by fisheries scientists that have nevertheless collapsed. The western Atlantic cod fishery is the most spectacular recent collapse. While it was a hugely productive fishery for 400 years, the introduction of modern factory trawlers in the 1980s and the pressure on the fishery led to it becoming unsustainable. The causes of fishery collapse are both economic and political in nature. Most fisheries are managed as a common (shared) resource even when the fishing territory lies within a country's territorial waters. Common resources are subject to an economic pressure known as the **tragedy of the commons** in which essentially no fisher has a motivation to exercise restraint in harvesting a fishery when it is not owned by that fisher. The natural outcome of harvests of resources held in common is their overexploitation. While large fisheries are regulated to attempt to avoid this pressure, it still exists in the background. This

overexploitation is exacerbated when access to the fishery is open and unregulated and when technology gives fishers the ability to overfish. In a few fisheries, the biological growth of the resource is less than the potential growth of the profits made from fishing if that time and money were invested elsewhere. In these cases—whales are an example—economic forces will always drive toward fishing the population to extinction.

Link to Learning

Explore a U.S. Fish & Wildlife Service interactive map of critical habitat for endangered and threatened species in the United States. To begin, select “Visit the online mapper.”

For the most part, fishery extinction is not equivalent to biological extinction—the last fish of a species is rarely fished out of the ocean. At the same

time, fishery extinction is still harmful to fish species and their ecosystems. There are some instances in which true extinction is a possibility. Whales have slow-growing populations and are at risk of complete extinction through hunting. There are some species of sharks with restricted distributions that are at risk of extinction. The groupers are another population of generally slow-growing fishes that, in the Caribbean, includes a number of species that are at risk of extinction from overfishing.

Coral reefs are extremely diverse marine ecosystems that face peril from several processes. Reefs are home to 1/3 of the world's marine fish species—about 4,000 species—despite making up only 1 percent of marine habitat. Most home marine aquaria are stocked with wild-caught organisms, not cultured organisms. Although no species is known to have been driven extinct by the pet trade in marine species, there are studies showing that populations of some species have declined in response to harvesting, indicating that the harvest is not sustainable at those levels. There are concerns about the effect of the pet trade on some terrestrial species such as turtles, amphibians, birds, plants, and even the orangutan.

Link to Learning

View a brief video discussing the role of marine ecosystems in supporting human welfare and the decline of ocean ecosystems.

Bush meat is the generic term used for wild animals killed for food. Hunting is practiced throughout the world, but hunting practices, particularly in equatorial Africa and parts of Asia, are believed to threaten several species with extinction. Traditionally, bush meat in Africa was hunted to feed families directly; however, recent commercialization of the practice now has bush meat available in grocery stores, which has increased harvest rates to the level of unsustainability. Additionally, human population growth has increased the need for protein foods that are not being met from agriculture. Species threatened by the bush meat trade are mostly mammals including many primates living in the Congo basin.

The brown tree snake, *Boiga irregularis*, is an exotic

species that has caused numerous extinctions on the island of Guam since its accidental introduction in 1950. (credit: NPS)This Limosa Harlequin Frog (*Atelopus limosus*), an endangered species from Panama, died from a fungal disease called chytridiomycosis. The red lesions are symptomatic of the disease. (credit: Brian Gratwicke)This little brown bat in Greeley Mine, Vermont, March 26, 2009, was found to have white-nose syndrome. (credit: Marvin Moriarty, USFWS)

Exotic Species

Exotic species are species that have been intentionally or unintentionally introduced by humans into an ecosystem in which they did not evolve. Such introductions likely occur frequently as natural phenomena. For example, Kudzu (*Pueraria lobata*), which is native to Japan, was introduced in the United States in 1876. It was later planted for soil conservation. Problematically, it grows too well in the southeastern United States—up to a foot a day. It is now a pest species and covers over 7 million acres in the southeastern United States. If an introduced species is able to survive in its new habitat, that introduction is now reflected in the observed range of the species. Human transportation of people and goods, including the intentional transport of organisms for trade, has dramatically increased the introduction of species into new ecosystems, sometimes at distances that are well

beyond the capacity of the species to ever travel itself and outside the range of the species' natural predators.

Most exotic species introductions probably fail because of the low number of individuals introduced or poor adaptation to the ecosystem they enter. Some species, however, possess preadaptations that can make them especially successful in a new ecosystem. These exotic species often undergo dramatic population increases in their new habitat and reset the ecological conditions in the new environment, threatening the species that exist there. For this reason, exotic species are also called invasive species. Exotic species can threaten other species through competition for resources, predation, or disease.

Link to Learning

Explore an interactive global database of exotic or invasive species.

Lakes and islands are particularly vulnerable to extinction threats from introduced species. In Lake Victoria, as mentioned earlier, the intentional introduction of the Nile perch was largely responsible for the extinction of about 200 species of cichlids. The accidental introduction of the brown tree snake via aircraft ([link]) from the Solomon Islands to Guam in 1950 has led to the extinction of three species of birds and three to five species of reptiles endemic to the island. Several other species are still threatened. The brown tree snake is adept at exploiting human transportation as a means to migrate; one was even found on an aircraft arriving in Corpus Christi, Texas. Constant vigilance on the part of airport, military, and commercial aircraft personnel is required to prevent the snake from moving from Guam to other islands in the Pacific, especially Hawaii. Islands do not make up a large area of land on the globe, but they do contain a disproportionate number of endemic species because of their isolation from mainland ancestors.

It now appears that the global decline in amphibian species recognized in the 1990s is, in some part, caused by the fungus *Batrachochytrium dendrobatidis*, which causes the disease **chytridiomycosis** ([link]). There is evidence that the fungus is native to Africa and may have been spread throughout the world by transport of a commonly used laboratory and pet species: the African clawed toad (*Xenopus laevis*). It may well be that biologists themselves are responsible for spreading this disease worldwide. The North American bullfrog, *Rana catesbeiana*, which has also been widely introduced as a food animal but which easily escapes captivity, survives most infections of *Batrachochytrium dendrobatidis* and can act as a reservoir for the disease.

Early evidence suggests that another fungal pathogen, *Geomyces destructans*, introduced from Europe is responsible for **white-nose syndrome**, which infects cave-hibernating bats in eastern North America and has spread from a point of origin in western New York State ([link]). The disease has decimated bat populations and threatens extinction of species already listed as endangered: the Indiana bat, *Myotis sodalis*, and potentially the Virginia big-eared bat, *Corynorhinus townsendii virginianus*. How the fungus was introduced is unclear, but one

logical presumption would be that recreational cavers unintentionally brought the fungus on clothes or equipment from Europe.

Since 2008, grizzly bears (*Ursus arctos horribilis*) have been spotted farther north than their historic range, a possible consequence of climate change. As a result, grizzly bear habitat now overlaps polar bear (*Ursus maritimus*) habitat. The two kinds of bears, which are capable of mating and producing viable offspring, are considered separate species as historically they lived in different habitats and never met. However, in 2006 a hunter shot a wild grizzly-polar bear hybrid known as a grolar bear, the first

wild hybrid ever found.

Climate Change

Climate change, and specifically the anthropogenic (meaning, caused by humans) warming trend presently underway, is recognized as a major extinction threat, particularly when combined with other threats such as habitat loss. Scientists disagree about the likely magnitude of the effects, with extinction rate estimates ranging from 15 percent to 40 percent of species committed to extinction by 2050. Scientists do agree, however, that climate change will alter regional climates, including rainfall and snowfall patterns, making habitats less hospitable to the species living in them. The warming trend will shift colder climates toward the north and south poles, forcing species to move with their adapted climate norms while facing habitat gaps along the way. The shifting ranges will impose new competitive regimes on species as they find themselves in contact with other species not present in their historic range. One such unexpected species contact is between polar bears and grizzly bears. Previously, these two species had separate ranges. Now, their ranges are overlapping and there are documented cases of these two species mating and producing viable offspring. Changing climates also throw off species' delicate timing adaptations to seasonal food resources and breeding times. Many contemporary mismatches to shifts in resource

availability and timing have already been documented.

Range shifts are already being observed: for example, some European bird species ranges have moved 91 km northward. The same study suggested that the optimal shift based on warming trends was

double that distance, suggesting that the populations are not moving quickly enough. Range shifts have also been observed in plants, butterflies, other insects, freshwater fishes, reptiles, and mammals.

Climate gradients will also move up mountains, eventually crowding species higher in altitude and eliminating the habitat for those species adapted to the highest elevations. Some climates will completely disappear. The rate of warming appears to be accelerated in the arctic, which is recognized as a serious threat to polar bear populations that require sea ice to hunt seals during the winter months: seals are the only source of protein available to polar bears. A trend to decreasing sea ice coverage has occurred since observations began in the mid-twentieth century. The rate of decline observed in recent years is far greater than previously predicted by climate models.

Finally, global warming will raise ocean levels due to melt water from glaciers and the greater volume of warmer water. Shorelines will be inundated, reducing island size, which will have an effect on some species, and a number of islands will disappear entirely. Additionally, the gradual melting and subsequent refreezing of the poles, glaciers, and higher elevation mountains—a cycle that has provided freshwater to environments for centuries—will also be jeopardized. This could result in an

overabundance of salt water and a shortage of fresh water.

Section Summary

The core threats to biodiversity are human population growth and unsustainable resource use. To date, the most significant causes of extinctions are habitat loss, introduction of exotic species, and overharvesting. Climate change is predicted to be a significant cause of extinctions in the coming century. Habitat loss occurs through deforestation, damming of rivers, and other activities. Overharvesting is a threat particularly to aquatic species, while the taking of bush meat in the humid tropics threatens many species in Asia, Africa, and the Americas. Exotic species have been the cause of a number of extinctions and are especially damaging to islands and lakes. Exotic species' introductions are increasing because of the increased mobility of human populations and growing global trade and transportation. Climate change is forcing range changes that may lead to extinction. It is also affecting adaptations to the timing of resource availability that negatively affects species in seasonal environments. The impacts of climate change are greatest in the arctic. Global warming will also raise sea levels, eliminating some islands and reducing the area of all others.

Art Connections

Converting a prairie to a farm field is an example of _____.

1. overharvesting
2. habitat loss
3. exotic species
4. climate change

B

Review Questions

Which two extinction risks may be a direct result of the pet trade?

1. climate change and exotic species introduction
2. habitat loss and overharvesting
3. overharvesting and exotic species introduction
4. habitat loss and climate change

C

Exotic species are especially threatening to what kind of ecosystem?

1. deserts
2. marine ecosystems
3. islands
4. tropical forests

C

Free Response

Describe the mechanisms by which human population growth and resource use causes increased extinction rates.

Human population growth leads to unsustainable resource use, which causes habitat destruction to build new human settlements, create agricultural fields, and so on. Larger human populations have also led to unsustainable fishing and hunting of wild animal populations. Excessive use of fossil fuels also leads to global warming.

Explain what extinction threats a frog living on a mountainside in Costa Rica might face.

The frog is at risk from global warming shifting its preferred habitat up the mountain. In addition, it will be at risk from exotic species, either as a new predator or through the impact of transmitted diseases such as chytridiomycosis. It is also possible that habitat destruction will threaten the species.

Glossary

bush meat
: wild-caught animal used as food (typically mammals, birds, and reptiles); usually referring to hunting in the tropics of sub-Saharan Africa, Asia, and the Americas

chytridiomycosis
: disease of amphibians caused by the fungus *Batrachochytrium dendrobatidis;* thought to be a major cause of the global amphibian decline

exotic species
: (also, invasive species) species that has been introduced to an ecosystem in which it did not evolve

tragedy of the commons

economic principle that resources held in common will inevitably be overexploited

white-nose syndrome
: disease of cave-hibernating bats in the eastern United States and Canada associated with the fungus *Geomyces destructans*

Preserving Biodiversity
By the end of this section, you will be able to:

- Identify new technologies for describing biodiversity
- Explain the legislative framework for conservation
- Describe principles and challenges of conservation preserve design
- Identify examples of the effects of habitat restoration
- Discuss the role of zoos in biodiversity conservation

Preserving biodiversity is an extraordinary challenge that must be met by greater understanding of biodiversity itself, changes in human behavior and beliefs, and various preservation strategies.

Measuring Biodiversity

The technology of molecular genetics and data processing and storage are maturing to the point where cataloguing the planet's species in an accessible way is close to feasible. **DNA barcoding** is one molecular genetic method, which takes advantage of rapid evolution in a mitochondrial gene present in eukaryotes, excepting the plants, to identify species using the sequence of portions of

the gene. Plants may be barcoded using a combination of chloroplast genes. Rapid mass sequencing machines make the molecular genetics portion of the work relatively inexpensive and quick. Computer resources store and make available the large volumes of data. Projects are currently underway to use DNA barcoding to catalog museum specimens, which have already been named and studied, as well as testing the method on less studied groups. As of mid 2012, close to 150,000 named species had been barcoded. Early studies suggest there are significant numbers of undescribed species that looked too much like sibling species to previously be recognized as different. These now can be identified with DNA barcoding.

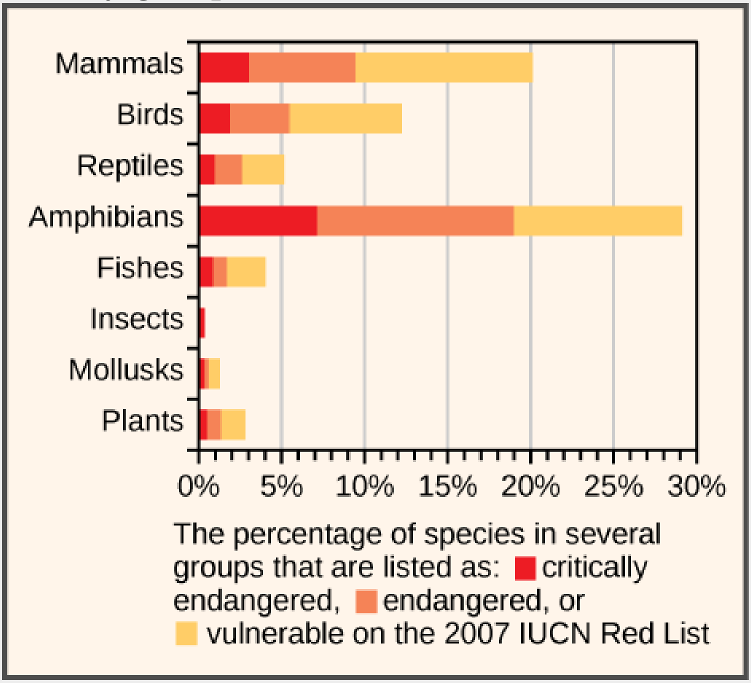
Numerous computer databases now provide information about named species and a framework for adding new species. However, as already noted, at the present rate of description of new species, it will take close to 500 years before the complete catalog of life is known. Many, perhaps most, species on the planet do not have that much time.

There is also the problem of understanding which species known to science are threatened and to what degree they are threatened. This task is carried out by the non-profit IUCN which, as previously mentioned, maintains the Red List—an online listing of endangered species categorized by taxonomy, type of threat, and other criteria ([link]). The Red

List is supported by scientific research. In 2011, the list contained 61,000 species, all with supporting documentation.

Art Connection

This chart shows the percentage of various animal species, by group, on the IUCN Red List as of 2007.



Which of the following statements is not supported by this graph?

1. There are more vulnerable fishes than critically endangered and endangered fishes combined.
2. There are more critically endangered

amphibians than vulnerable, endangered and critically endangered reptiles combined.
3. Within each group, there are more critically endangered species than vulnerable species.
4. A greater percentage of bird species are critically endangered than mollusk species.

Changing Human Behavior

Legislation throughout the world has been enacted to protect species. The legislation includes international treaties as well as national and state laws. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) treaty came into force in 1975. The treaty, and the national legislation that supports it, provides a legal framework for preventing approximately 33,000 listed species from being transported across nations' borders, thus protecting them from being caught or killed when international trade is involved. The treaty is limited in its reach because it only deals with international movement of organisms or their parts. It is also limited by various countries' ability or willingness to enforce the treaty and supporting legislation. The illegal trade in organisms and their parts is probably a market in the hundreds of millions of dollars. Illegal

wildlife trade is monitored by another non-profit: Trade Records Analysis of Flora and Fauna in Commerce (TRAFFIC).

Within many countries there are laws that protect endangered species and regulate hunting and fishing. In the United States, the Endangered Species Act (ESA) was enacted in 1973. Species at risk are listed by the Act; the U.S. Fish & Wildlife Service is required by law to develop management plans that protect the listed species and bring them back to sustainable numbers. The Act, and others like it in other countries, is a useful tool, but it suffers because it is often difficult to get a species listed, or to get an effective management plan in place once it is listed. Additionally, species may be controversially taken off the list without necessarily having had a change in their situation. More fundamentally, the approach to protecting individual species rather than entire ecosystems is both inefficient and focuses efforts on a few highly visible and often charismatic species, perhaps at the expense of other species that go unprotected. At the same time, the Act has a critical habitat provision outlined in the recovery mechanism that may benefit species other than the one targeted for management.

The Migratory Bird Treaty Act (MBTA) is an agreement between the United States and Canada that was signed into law in 1918 in response to

declines in North American bird species caused by hunting. The Act now lists over 800 protected species. It makes it illegal to disturb or kill the protected species or distribute their parts (much of the hunting of birds in the past was for their feathers).

The international response to global warming has been mixed. The Kyoto Protocol, an international agreement that came out of the United Nations Framework Convention on Climate Change that committed countries to reducing greenhouse gas emissions by 2012, was ratified by some countries, but spurned by others. Two important countries in terms of their potential impact that did not ratify the Kyoto Protocol were the United States and China. The United States rejected it as a result of a powerful fossil fuel industry and China because of a concern it would stifle the nation's growth. Some goals for reduction in greenhouse gasses were met and exceeded by individual countries, but worldwide, the effort to limit greenhouse gas production is not succeeding. The intended replacement for the Kyoto Protocol has not materialized because governments cannot agree on timelines and benchmarks. Meanwhile, climate scientists predict the resulting costs to human societies and biodiversity will be high.

As already mentioned, the private non-profit sector plays a large role in the conservation effort both in

North America and around the world. The approaches range from species-specific organizations to the broadly focused IUCN and TRAFFIC. The Nature Conservancy takes a novel approach. It purchases land and protects it in an attempt to set up preserves for ecosystems. Ultimately, human behavior will change when human values change. At present, the growing urbanization of the human population is a force that poses challenges to the valuing of biodiversity. Robert H. MacArthur and Edward O. Wilson, E. O., *The Theory of Island Biogeography* (Princeton, N.J.: Princeton University Press, 1967). (a) The Gibbon wolf pack in Yellowstone National Park, March 1, 2007, represents a keystone species. The reintroduction of wolves into Yellowstone National Park in 1995 led to a change in the grazing behavior of (b) elk. To avoid predation, the elk no longer grazed exposed stream and riverbeds, such as (c) the Lamar Riverbed in Yellowstone. This allowed willow and cottonwood seedlings to grow. The seedlings decreased erosion and provided shading to the creek, which improved fish habitat. A new colony of (d) beaver may also have benefited from the habitat change. (credit a: modification of work by Doug Smith, NPS; credit c: modification of work by Jim Peaco, NPS; credit d: modification of work by "Shiny Things"/Flickr)

Conservation in Preserves

Establishment of wildlife and ecosystem preserves is one of the key tools in conservation efforts. A preserve is an area of land set aside with varying degrees of protection for the organisms that exist within the boundaries of the preserve. Preserves can be effective in the short term for protecting both species and ecosystems, but they face challenges that scientists are still exploring to strengthen their viability as long-term solutions.

How Much Area to Preserve?

Due to the way protected lands are allocated (they tend to contain less economically valuable resources rather than being set aside specifically for the species or ecosystems at risk) and the way biodiversity is distributed, determining a target percentage of land or marine habitat that should be protected to maintain biodiversity levels is challenging. The IUCN World Parks Congress estimated that 11.5 percent of Earth's land surface was covered by preserves of various kinds in 2003. This area is greater than previous goals; however, it only represents 9 out of 14 recognized major biomes. Research has shown that 12 percent of all species live only outside preserves; these percentages are much higher when only threatened species and high quality preserves are considered. For example, high quality preserves include only about 50 percent of threatened amphibian species. The conclusion must be that either the percentage of

area protected must increase, or the percentage of high quality preserves must increase, or preserves must be targeted with greater attention to biodiversity protection. Researchers argue that more attention to the latter solution is required.

Preserve Design

There has been extensive research into optimal preserve designs for maintaining biodiversity. The fundamental principle behind much of the research has been the seminal theoretical work of Robert H. MacArthur and Edward O. Wilson published in 1967 on island biogeography.[footnote] This work sought to understand the factors affecting biodiversity on islands. The fundamental conclusion was that biodiversity on an island was a function of the origin of species through migration, speciation, and extinction on that island. Islands farther from a mainland are harder to get to, so migration is lower and the equilibrium number of species is lower. Within island populations, evidence suggests that the number of species gradually increases to a level similar to the numbers on the mainland from which the species is suspected to have migrated. In addition, smaller islands are harder to find, so their immigration rates for new species are lower. Smaller islands are also less geographically diverse so there are fewer niches to promote speciation. And finally, smaller islands support smaller populations, so the probability of extinction is higher.

As islands get larger, the number of species accelerates, although the effect of island area on species numbers is not a direct correlation. Conservation preserves can be seen as “islands” of habitat within “an ocean” of non-habitat. For a species to persist in a preserve, the preserve must be large enough. The critical size depends, in part, on the home range that is characteristic of the species. A preserve for wolves, which range hundreds of kilometers, must be much larger than a preserve for butterflies, which might range within ten kilometers during its lifetime. But larger preserves have more core area of optimal habitat for individual species, they have more niches to support more species, and they attract more species because they can be found and reached more easily.

Preserves perform better when there are buffer zones around them of suboptimal habitat. The buffer allows organisms to exit the boundaries of the preserve without immediate negative consequences from predation or lack of resources. One large preserve is better than the same area of several smaller preserves because there is more core habitat unaffected by edges. For this same reason, preserves in the shape of a square or circle will be better than a preserve with many thin “arms.” If preserves must be smaller, then providing wildlife corridors between them so that individuals and their genes can move between the preserves, for example along rivers and streams, will make the smaller preserves

behave more like a large one. All of these factors are taken into consideration when planning the nature of a preserve before the land is set aside.

In addition to the physical, biological, and ecological specifications of a preserve, there are a variety of policy, legislative, and enforcement specifications related to uses of the preserve for functions other than protection of species. These can include anything from timber extraction, mineral extraction, regulated hunting, human habitation, and nondestructive human recreation. Many of these policy decisions are made based on political pressures rather than conservation considerations. In some cases, wildlife protection policies have been so strict that subsistence-living indigenous populations have been forced from ancestral lands that fell within a preserve. In other cases, even if a preserve is designed to protect wildlife, if the protections are not or cannot be enforced, the preserve status will have little meaning in the face of illegal poaching and timber extraction. This is a widespread problem with preserves in areas of the tropics.

Limitations on Preserves

Some of the limitations on preserves as conservation tools are evident from the discussion of preserve design. Political and economic pressures typically make preserves smaller, never larger, so setting

aside areas that are large enough is difficult. If the area set aside is sufficiently large, there may not be sufficient area to create a buffer around the preserve. In this case, an area on the outer edges of the preserve inevitably becomes a riskier suboptimal habitat for the species in the preserve. Enforcement of protections is also a significant issue in countries without the resources or political will to prevent poaching and illegal resource extraction.

Climate change will create inevitable problems with the location of preserves. The species within them will migrate to higher latitudes as the habitat of the preserve becomes less favorable. Scientists are planning for the effects of global warming on future preserves and striving to predict the need for new preserves to accommodate anticipated changes to habitats; however, the end effectiveness is tenuous since these efforts are prediction based.

Finally, an argument can be made that conservation preserves reinforce the cultural perception that humans are separate from nature, can exist outside of it, and can only operate in ways that do damage to biodiversity. Creating preserves reduces the pressure on human activities outside the preserves to be sustainable and non-damaging to biodiversity. Ultimately, the political, economic, and human demographic pressures will degrade and reduce the size of conservation preserves if the activities outside them are not altered to be less damaging to

biodiversity.

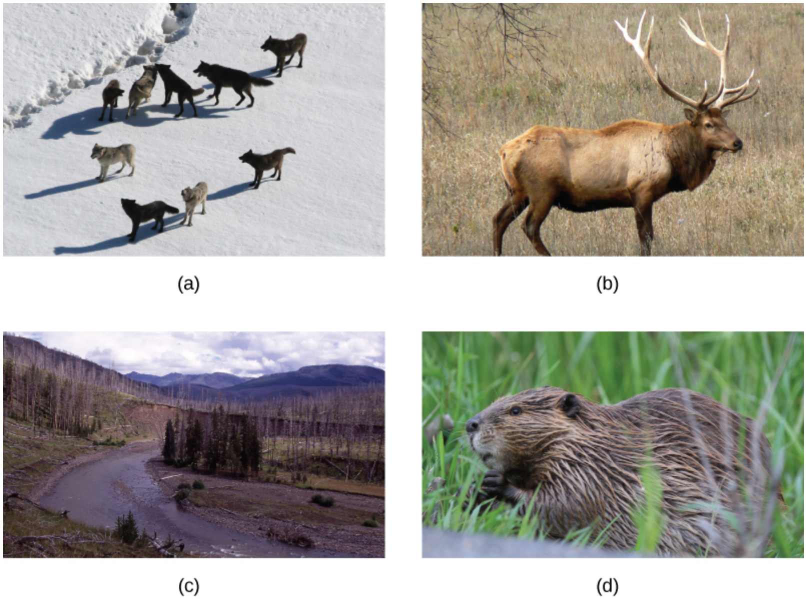
Link to Learning

An interactive global data system of protected areas can be found at website. Review data about individual protected areas by location or study statistics on protected areas by country or region.

Habitat Restoration

Habitat restoration holds considerable promise as a mechanism for restoring and maintaining biodiversity. Of course once a species has become extinct, its restoration is impossible. However, restoration can improve the biodiversity of degraded ecosystems. Reintroducing wolves, a top predator, to Yellowstone National Park in 1995 led to dramatic changes in the ecosystem that increased biodiversity. The wolves ([link]) function to

suppress elk and coyote populations and provide more abundant resources to the guild of carrion eaters. Reducing elk populations has allowed revegetation of riparian areas, which has increased the diversity of species in that habitat. Decreasing the coyote population has increased the populations of species that were previously suppressed by this predator. The number of species of carrion eaters has increased because of the predatory activities of the wolves. In this habitat, the wolf is a keystone species, meaning a species that is instrumental in maintaining diversity in an ecosystem. Removing a keystone species from an ecological community may cause a collapse in diversity. The results from the Yellowstone experiment suggest that restoring a keystone species can have the effect of restoring biodiversity in the community. Ecologists have argued for the identification of keystone species where possible and for focusing protection efforts on those species; likewise, it also makes sense to attempt to return them to their ecosystem if they have been removed.



Other large-scale restoration experiments underway involve dam removal. In the United States, since the mid-1980s, many aging dams are being considered for removal rather than replacement because of shifting beliefs about the ecological value of free-flowing rivers and because many dams no longer provide the benefit and functions that they did when they were first built. The measured benefits of dam removal include restoration of naturally fluctuating water levels (the purpose of dams is frequently to reduce variation in river flows), which leads to increased fish diversity and improved water quality. In the Pacific Northwest, dam removal projects are expected to increase populations of salmon, which is considered a keystone species because it transports key nutrients to inland ecosystems during its annual spawning migrations.

In other regions such as the Atlantic coast, dam removal has allowed the return of spawning anadromous fish species (species that are born in fresh water, live most of their lives in salt water, and return to fresh water to spawn). Some of the largest dam removal projects have yet to occur or have happened too recently for the consequences to be measured. The large-scale ecological experiments that these removal projects constitute will provide valuable data for other dam projects slated either for removal or construction.

The Role of Captive Breeding

Zoos have sought to play a role in conservation efforts both through captive breeding programs and education. The transformation of the missions of zoos from collection and exhibition facilities to organizations that are dedicated to conservation is ongoing. In general, it has been recognized that, except in some specific targeted cases, captive breeding programs for endangered species are inefficient and often prone to failure when the species are reintroduced to the wild. Zoo facilities are far too limited to contemplate captive breeding programs for the numbers of species that are now at risk. Education is another potential positive impact of zoos on conservation efforts, particularly given the global trend to urbanization and the consequent reduction in contacts between people and wildlife. A number of studies have been performed to look at

the effectiveness of zoos on people's attitudes and actions regarding conservation; at present, the results tend to be mixed.

Section Summary

New technological methods such as DNA barcoding and information processing and accessibility are facilitating the cataloging of the planet's biodiversity. There is also a legislative framework for biodiversity protection. International treaties such as CITES regulate the transportation of endangered species across international borders. Legislation within individual countries protecting species and agreements on global warming have had limited success; there is at present no international agreement on targets for greenhouse gas emissions. In the United States, the Endangered Species Act protects listed species but is hampered by procedural difficulties and a focus on individual species. The Migratory Bird Act is an agreement between Canada and the United States to protect migratory birds. The non-profit sector is also very active in conservation efforts in a variety of ways.

Conservation preserves are a major tool in biodiversity protection. Presently, 11percent of Earth's land surface is protected in some way. The science of island biogeography has informed the optimal design of preserves; however, preserves have limitations imposed by political and economic

forces. In addition, climate change will limit the effectiveness of preserves in the future. A downside of preserves is that they may lessen the pressure on human societies to function more sustainably outside the preserves.

Habitat restoration has the potential to restore ecosystems to previous biodiversity levels before species become extinct. Examples of restoration include reintroduction of keystone species and removal of dams on rivers. Zoos have attempted to take a more active role in conservation and can have a limited role in captive breeding programs. Zoos also may have a useful role in education.

Art Connections

[link] Which of the following statements is not supported by this graph?

1. There are more vulnerable fishes than critically endangered and endangered fishes combined.
2. There are more critically endangered amphibians than vulnerable, endangered and critically endangered reptiles combined.
3. Within each group, there are more critically endangered species than vulnerable species.

4. A greater percentage of bird species are critically endangered than mollusk species.

[link] C

Review Questions

Certain parrot species cannot be brought to the United States to be sold as pets. What is the name of the legislation that makes this illegal?

1. Red List
2. Migratory Bird Act
3. CITES
4. Endangered Species Act (ESA)

C

What was the name of the first international agreement on climate change?

1. Red List
2. Montreal Protocol
3. International Union for the Conservation of Nature (IUCN)

4. Kyoto Protocol

D

About what percentage of land on the planet is set aside as a preserve of some type?

1. 1 percent
2. 6 percent
3. 11 percent
4. 15 percent

C

Free Response

Describe two considerations in conservation preserve design.

Larger preserves will contain more species. Preserves should have a buffer around them to protect species from edge effects. Preserves that are round or square are better than preserves with many thin arms.

Describe what happens to an ecosystem when a keystone species is removed.

When a keystone species is removed many species will disappear from the ecosystem.

Glossary

DNA barcoding
: molecular genetic method for identifying a unique genetic sequence to associate with a species